

COLONIAL PHILLIPSASTRAEIDAE FROM THE
DEVONIAN OF SOUTH-EAST DEVON, ENGLAND



BY
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By C. T. SCRUTTON

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SYNOPSIS

The classification of the family Phillipsastraeidae Roemer is critically reviewed. Twelve species belonging to the genera *Phillipsastrea*, *Frechastraea* gen. nov., *Thamnophyllum* and *Peneckiella*, and including *Phillipsastrea hennahi ussheri* subsp. nov., *P. rozkowskiae* sp. nov.,

Frechastrea carinata sp. nov., *Thamnophyllum caespitosum paucitabulatum* subsp. nov. and *Peneckiella salternensis* sp. nov. are described from the Middle and Upper Devonian of the Torquay, Paignton and Newton Abbot areas of south-east Devon. New names are proposed for *Thamnophyllum trigeminum* Penecke and *Macgeea* (*Thamnophyllum*) *minima* Schouppé. Detailed statistical studies of variation in species and subspecies samples and individual colonies of many of the taxa are described and analysed. The stratigraphy of the more important localities from which phillipsastreaeids have been collected is briefly reviewed.

I. INTRODUCTION

Not until the work of Schouppé (1958), over one hundred years after Lonsdale (1840) had erected "*Astrea hennahii*", was the presence of horseshoe dissepiments in this, the type species of the genus *Phillipsastrea* generally accepted. An earlier record of this fact by Smith (1945 : 37), who placed very little emphasis upon it, appears to have passed without notice. Schouppé, however, considered dissepimental form and the associated trabecular structure to be of particular taxonomic importance in the group of Devonian rugose corals with which *Phillipsastrea* is associated. He thus attempted a thorough revision of their classification, but his suggestions are, in part, unacceptable where they bring together species with markedly different morphological characteristics, unlikely to have been closely related.

The type locality of "*Astrea hennahii*" is Barton Quarry, Torquay (south Devon) and many of the colonial species and genera closely related to *Phillipsastrea* are also well represented in this area. These English corals have not been examined in detail since the middle of the last century, when Edwards & Haime (1853) described them, and their taxonomic revision is long overdue.

In the present paper the classification of the phillipsastreids is critically surveyed and the colonial species and genera of the Phillipsastraeidae from south-east Devon are described. As far as the material allows, the variation in the taxa described has been investigated statistically. Data collected for individual colonies of most of the species and subspecies enable, in addition, some comparisons to be made between specific and colonial variation.

In the course of this work it has been necessary to examine a number of species formerly considered as phillipsastreids, but which are now removed from the Phillipsastraeidae. These corals all belong to the family Marisastridae and have been described elsewhere (Scrutton 1967).

The following abbreviations are used: BM(NH) British Museum (Natural History); OUM University Museum, Oxford; GSM Geological Survey Museum, London; TM Torquay Museum; TM(JB) Jukes-Browne Collection in the Torquay Museum; GVM Dr. G. V. Middleton's Collection, Murchison Museum, Imperial College, London.

II. ACKNOWLEDGMENTS

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The author is particularly grateful to Professor M. R. House (Hull) who supervised the work and to Professor Maria Różkowska (Poznań, Poland) and to the late

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Mr. M. Mitchell (Institute of Geological Sciences, London) and Dr. G. F. Elliott have kindly read and criticized the palaeontological and stratigraphical sections of the manuscript respectively.

III. STRATIGRAPHY

A detailed account of the Devonian stratigraphy of south-east Devon is outside the scope of this work. As the vast majority of the material described comes from only six localities, however, it is intended to give a brief account of them here. They are confined to the limestones in the Torquay, Paignton and Newton Abbot areas (see Text-figs. 1, 2). Further general information on the geology of south-east Devon can be obtained from the Geological Survey Memoirs (Ussher 1903; Ussher *et al.* 1913; Lloyd 1933).

(a) Middle Devonian.

Dyer's Quarry (SX 92206280) is situated in the coastal cliffs at the western end of the Daddy Hole limestone mass. Exposed to sea level in the floor of the disused quarry is a 15 ft. sequence of thin-bedded, black, crinoidal limestones exceedingly rich in coral remains, overlain by virtually unfossiliferous limestones becoming lighter in colour and more massive towards the top of the quarry. The total thickness of exposed rock is about 60 to 70 ft.

The coral fauna in the floor of the quarry was mentioned briefly by Scrutton (1965 : 186) who suggested for it a lower Middle Givetian age. It is dominated by colonies of *Thamnophyllum germanicum schoupppei* nom. nov. (see p. 120), relatively unbroken and apparently preserved in their position of growth. Some of the simple corals also appear to retain their growth orientation. This suggests a sheltered environment, either protected from, or situated below the effects of strong wave action, as the large slender branching colonies of *Thamnophyllum* must have been rather delicate structures during life. The horizon with abundant *Thamnophyllum* is sharply succeeded by dark limestones with few solitary corals. Just above the junction is a thin band containing rounded limestone pebbles which probably represents contemporaneous erosion of the sea floor by wave action.

Wolborough Quarry (SX 85237042), in the south-west outskirts of Newton Abbot, has produced a large and varied fauna of Middle Devonian aspect in the past (Whidborne 1888-1907; Ussher *et al.* 1913 : 22-24) although corals have received little mention. Today, however, it is badly overgrown and the accessible outcrops yield only scattered fossils. The quarry is cut in massive, irregularly jointed limestones, usually coarsely crystalline, with a considerable bioclastic content and variously coloured from dark grey to a very pale yellowish tint.

Phillipsastrea devoniensis (Edwards & Haime) has been recorded from Wolborough and *Billingsastrea? battersbyi* (Edwards & Haime) (see Scrutton 1967 : 277) seems to have been fairly common there in the past. *Phillipsastrea hennahi hennahi*, a single specimen, and *Thamnophyllum caespitosum* (Goldfuss) have now been collected from the quarry together with scattered solitary corals including *Stringophyllum* sp.

The exact stratigraphical position of the Wolborough limestone was held to be uncertain by Ussher *et al.* (1913), but House (1963 : 5) has shown that the *Maenio-*

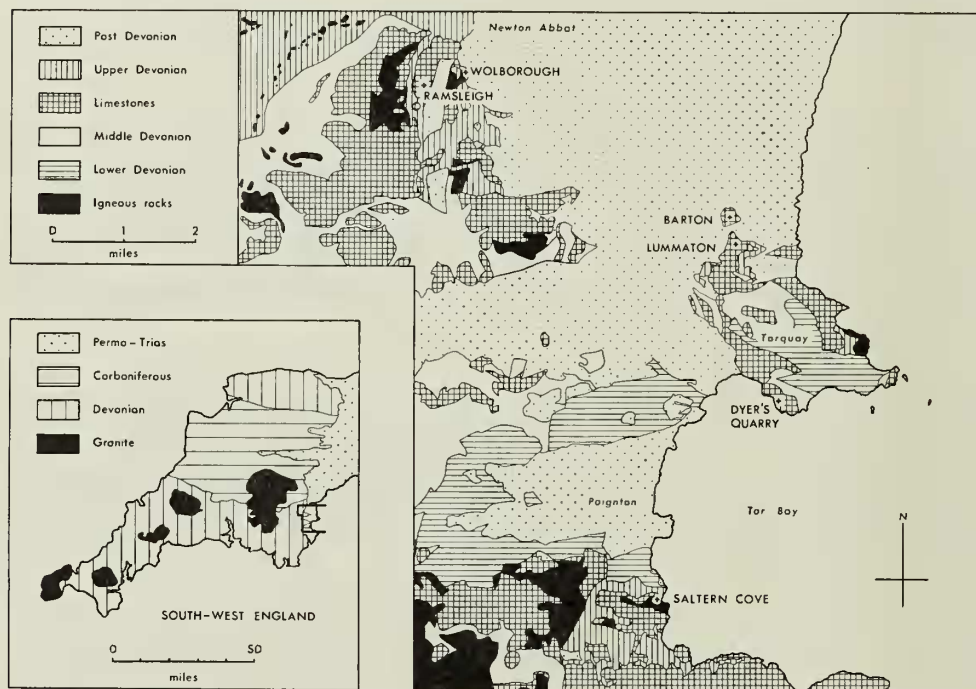


FIG. 1. Geological map of south-east Devon showing the main collection sites thus +. Inset map shows the position of the area (based on Geological Survey maps).

ceras molarium Zone of the middle Givetian is well developed here. Middleton (1959) unfortunately did not describe Wolborough representatives in his paper on south Devon tetracorals, but later (1960, table 1) he gave a general stratigraphical table for the Newton Abbot area based on a modified version of Wedekind's coral zones. It appears that the Wolborough limestone belongs to Middleton's Givetian "biostromal and clastic limestones" unit, separated, at least in part, from the "biohermal Frasnian limestone" of Ramsleigh Quarry and elsewhere by tuffs.

Lummaton Hill (SX 91306645). Probably more has been written about the series of quarries now within the northern outskirts of Torquay, than any other Devonian limestone exposure in the country. An early account of the lithologies and faunas in the quarries was given by Jukes-Browne (1906). Despite the massive

nature of the limestones, and the undoubted, though obscure, structural deformation, he suggested that a definite lithological succession could be established. Most of the lithological types—the massive stromatoporoid limestone, the grey shelly limestone of the Lummaton Shell Bed, and the bioclastic limestone of the more northern exposures—can still be recognized today. The rich and varied Lummaton fauna derives mainly from the Shell Bed and was monographed by Whidborne (1888–1907). The latter did not mention corals, but Jukes-Browne recorded *Phillipsastrea hennahi*

		STAGES	GONIATITE ZONES	TORQUAY		NEWTON ABBOT
DEVONIAN	UPPER	FAMENNIAN	CURVISPINA	OSTRACOD SLATE		
			HOLZAPFELI	SALTERN COVE BEDS	+ Goniatite horizon	
		FRASNIAN	CORDATUM		+ limestone with <i>Peneckeella</i>	RED SLATY LIMESTONE
			LUNULICOSTA	BABBACOMBE SLATES		BIOHERMAL LST. + Ramsleigh Quarry limestone
	MIDDLE	GIVETIAN	TEREBRATUM		+ Lummaton and Barton limestones	TUFFS
			MOLARIUM	TORQUAY LIMESTONE		
			ROUVILLEI	HOPE'S NOSE BEDS	+ Dyer's Quarry limestone	BIOSTROMAL and CLASTIC LIMESTONE
			JUGLERI	SHALES with <i>Calceola</i>		SLATE with fossils ? LST.
		COUVINIAN	LATESEPTATUS			SPILITIC ANDESITE
			WENKENBACHI	MEADFOOT and STADDON BEDS		
	LOWER	EMSIAN				

FIG. 2. Devonian successions for the Torquay area (modified after House & Selwood 1965) and the Newton Abbot area (modified after Middleton 1960).

hennahi and *Haplothecia pengellyi* (Edwards & Haime) from the bioclastic limestones in the northern end of the western quarries and noted that they did not occur elsewhere at Lummaton. Unfortunately, this particular locality has been worked out and these corals can no longer be collected here. They are still to be found, however, in limestones of a similar lithology exposed in nearby Barton Quarry.

Recent quarrying near the supposed strike of the Shell Bed has exposed a grey limestone with scattered brachiopods, tabulate and simple rugose corals, bryozoa and broken colonies of *Thamnophyllum caespitosum paucitabulatum* subsp. nov. This is the first record of *Thamnophyllum* from Lummaton. The lithology suggests that the horizon is above rather than below the Shell Bed.

The Lummaton fauna was described by Kayser (1889 : 186) as indicative of the upper beds of the Middle Devonian. Recent work has fully substantiated this. Elliott (1961 : 256 *et seq.*) commented on the apparent coexistence of *Stringocephalus*

burtini and “*Rhynchonella*” *cuboides*, held to be markers for the Givetian and Frasnian respectively on the Continent. This had caused Ussher *et al.* (1913 : 14) to consider the Lummaton limestones to be transitional across the Middle–Upper Devonian boundary. Elliott showed, however, that the “*cuboides*” from the Lummaton Shell Bed should be compared with the Upper Givetian *Hypothyridina procuboides* of Torley (1934) from Germany which strongly suggests a Middle Devonian age for this horizon. House (1963 : 6) later confirmed Elliott’s age for the Lummaton Shell Bed. He described a goniatite fauna from this level which can be correlated with the *terebratum* Zone of Upper Givetian age.

Elliott (1961 : 256) quoted the occurrence of *Phillipsastrea hennahi hennahi* at Lummaton and Barton as support for the presence of Frasnian rocks above the Givetian at both localities. Middleton (1959 : 156), however, had already recorded this subspecies from Middle Devonian (? upper *Sparganophyllum* Zone) limestones near Dartington Hall and it is recorded here from undoubted middle Givetian at Wolborough Quarry. Furthermore there is good evidence to suggest an upper Givetian age for the limestones at Barton from which *P. hennahi hennahi* can now be collected.

Barton Quarry (SX 91246710), about a quarter of a mile north of Lummaton, is now used as a caravan camp. The quarry is cut in massive, mainly dark-grey coarse crystalline bioclastic limestone which, in the past, has yielded a large and varied fauna monographed by Whidborne (1888–1907) and listed by Ussher *et al.* (1913 : 26). The former did not record the corals but Ussher *et al.* (1913 : 25) described finer textured parts of the limestone as abounding in corals and stromatopora. Most of the corals now seen are tabulates, mainly *Thamnopora* and *Alveolites* but it is still possible to collect a few specimens of *Phillipsastrea hennahi hennahi* and *Haplothechia pengellyi* together with *Acanthophyllum* sp. from the western wall of the old quarry.

Barton is the type locality for *P. hennahi*. The horizon has been considered Frasnian in age based on early Continental records of this subspecies from Upper Devonian rocks. House (1963 : 6), however, has identified *Wedekindella brilonense* (Kayser) from among Whidborne’s Barton fauna, presumably coming from the massive limestones of the quarry. This goniatite suggests the *terebratum* Zone and thus an upper Givetian age. In addition *Acanthophyllum* has not so far been recorded above the Middle Devonian. Thus the evidence supports an upper Givetian rather than a Frasnian age for the Barton limestones and on the grounds of lithological and faunal similarity, the beds that in the past yielded *P. hennahi hennahi* and *Haplothechia pengellyi* at Lummaton are probably of the same age.

(b) Upper Devonian.

The disused **Ramsleigh Quarry** (SX 84417015) is situated about a quarter of a mile east of East Ogwell, south-west of Newton Abbot. Exposed in the quarry and in the road cutting immediately to the south are massive, dominantly fine grained limestones, medium to pinky grey for the most part but with prominent lenses of a salmon pink colour.

The age of the Ramsleigh limestones has been considered as Frasnian since the

early eighteen eighties at least. Ussher *et al.* (1913 : 15) quoted from an unpublished manuscript written by Champernowne in which the latter considered that the "splendid Ramsleigh mass . . . is precisely the counterpart of the marble masses of the 'Étage de Frasné' in Belgium". A few years after Champernowne wrote this, Kayser (1889 : 186) correlated the Ramsleigh limestone with the Ibergerkalk of Germany. In more recent times, Dineley & Rhodes (1956 : 244) investigated a conodont fauna collected from a pale limestone band somewhat below the level in the quarry at which most of the massive corals are found. They concluded that the fauna was Lower Frasnian in age. Middleton (1959) briefly described some of the corals found in the quarry. Under his description of "*Phillipsastraea pentagona* var. *micrommata*" he wrote (p. 157) that "According to Rózkowska this variety is characteristic of the upper Frasnian". It is presumably on this basis that he considered (p. 156) the Ramsleigh limestone to be "probably middle or upper Frasnian" in age. Rózkowska (1953), however, makes no definite statement of the stratigraphical range of this coral, merely describing it from the upper Frasnian of Poland. Furthermore, although *Frechastraea carinata* sp. nov. (= *Phillipsastraea pentagona* var. *micrommata* of authors) does occur at Ramsleigh, Middleton misidentified his material which should correctly be assigned to *F. pentagona minima*. House (1963 : 6), on the evidence of ammonoids collected by Shannon from Ramsleigh Quarry, inferred that the *lunulicosta* Zone, the lowest goniatite zone in the Frasnian, is represented by the massive limestones. Thus the weight of the fossil evidence suggests that these beds are Lower Frasnian in age.

Quite a large and varied collection of massive corals has been made from the quarry and the adjacent road cutting. *Phillipsastraea hennahi ussheri* subsp. nov., *P. ananas* (Goldfuss), *P. rozkowskiae* sp. nov., *Frechastraea pentagona pentagona* (Goldfuss), *F. pentagona minima*, *F. carinata* sp. nov., *F. goldfussi* (de Verneuil & Haime) and *F. bowerbanki* (Edwards & Haime) are described in this paper and *Haplothecia ogwellensis* Scrutton elsewhere (Scrutton 1967 : 272). Most of the material recently collected came from the higher parts of the old quarry face and from a series of outcrops in the road cutting, between 20 and 80 yards west of the lane leading to the quarry.

Saltern Cove (SX 895585), on the shores of Tor Bay, is $1\frac{1}{2}$ miles south of Paignton. Resting on the altered doleritic rock, variously interpreted as a lava or a sill, which forms the southern horn of the cove, is a sequence of shales and limestones of Upper Devonian age (see Lloyd 1933 : 86 *et seq.*; House 1963 : 8; Scrutton 1965 : 188). Immediately above the igneous rock is about 20 ft. of thick bedded limestone with a distinctive band rich in broken colonies of *Peneckiella* at the base (SX 89505842). This is the "main *Peneckiella* horizon" referred to elsewhere in this paper. Higher in the succession intercalations of red shale become increasingly important, separating thinner beds of limestone which completely disappear some 50 ft. above the base of the sequence. The corals in these thin bedded limestones have been briefly mentioned by Scrutton (1965 : 188) as indicating a Frasnian age. With the presence of the *holzapfeli* Zone of Upper Frasnian age established in the northern end of the cove, the limestone horizons are probably within the Middle Frasnian *cordatum* Zone as inferred by House (1963 : 7-8).

IV. GENERAL PALAEONTOLOGY OF THE COLONIAL
PHILLIPSASTRAEIDAE

Features of the microstructure, increase and variation in the Phillipsastraeidae are sufficiently uniform to warrant general treatment. By so doing much repetition is saved in the systematic descriptions of individual species and subspecies. The terminology used in this and subsequent sections is that given by Moore, Hill & Wells (1956) unless otherwise indicated.

(a) Microstructure.

Slight recrystallization or deformation of coral material may easily obscure the details of fine structure in the skeletal tissue. Although the preservation of the English Devonian material is not particularly good, all the species and subspecies described here do show some details of their original microstructure.

The septa are characterized by a dark, irregular median line on either side of which are fibres of crystalline calcite (see for example Pl. 13, fig. 1). Where the preservation is best, the fibres can be seen arranged in paired tufts or fascicles on either side of the septal axis. Each pair is presumably the cross-section of a single monacanthine trabecula, with the successive centres of calcification in the fibre fascicles, and thus in the trabecular axes, forming the dark median line. It has not been possible, however, to distinguish clearly the boundaries of individual trabeculae in cross-section.

The structure is most clearly developed in the dilated part of each septum, in the zone immediately outside the tabularium. The dilatation appears to be the result of simple swelling of the trabeculae. There is never more than a slight offsetting of the centres of calcification—in other words, very little break-up or zigzagging of the dark median line—to suggest that the septa become multitrabecular.

The arrangement of the trabeculae in the vertical plane is reflected by the direction of divergence of the fibre fascicles from the median plane of the septum in cross-section (see Kato 1963, text-fig. 3). In the phillipsastraeids described here, the fibres can sometimes be clearly seen changing their attitude to face outwards at either end of the dilated part of the septum, corresponding to the fan-shaped divergence of the trabeculae in the septal plane. The point of divergence is located more or less centrally in the zone of septal dilatation.

The carination developed in *Frechastraea carinata* sp. nov. and *Peneckiella salternensis* sp. nov. is due to the development of regularly spaced, enlarged trabeculae. Whilst the trabeculae retain their linear arrangement along the septal axis the carinae are yard-arm, but they may become offset on alternate sides of the septum, resulting in xyloid carination. The swollen trabeculae are sometimes separated by clear structureless calcite as though the trabeculae had separated and the septa become discontinuous. To what extent this effect is the result of recrystallization is difficult to ascertain.

In longitudinal-section, the arrangement of the trabeculae in the septal plane can often be clearly seen (Text-figs. 3, 7b). As mentioned above, the trabeculae are arranged in a fan and this is centred on the crest of the dissepimentarium, usually formed by horseshoe or peneckielloid (Rózkowska 1960 : 32) dissepiments. In the

zone of septal dilatation, which is most frequently sectioned in a longitudinal slice, the trabecular fan may often appear symmetrical about the axis of divergence. When more rarely a longitudinal-section is obtained of the thinner parts of the septum, the symmetrical arrangement is not maintained. Particularly in the species of *Phillipsastrea* and *Frechastraea*, the trabeculae in the dissepimentarium gradually return to a vertical position as the septa are traced towards the periphery of the corallites. In the tabularium, septa are composed of trabeculae from the edge of the fan, entering from the dissepimentarium at a very low angle, often almost horizontally. The attitude of the trabeculae appears always to be normal to the dissepimental surface (Text-fig. 3).

In the case of *Thamnophyllum* (Text-fig. 7b), the evidence suggests that the trabecular fan is more nearly symmetrical in the septum although, in the major septa particularly, the centre of divergence is closer to the epithecal than the axial end. The fan in species of *Peneckiella* is somewhat less symmetrical and more variable in shape—a reflection of the diversification in dissepimental form.

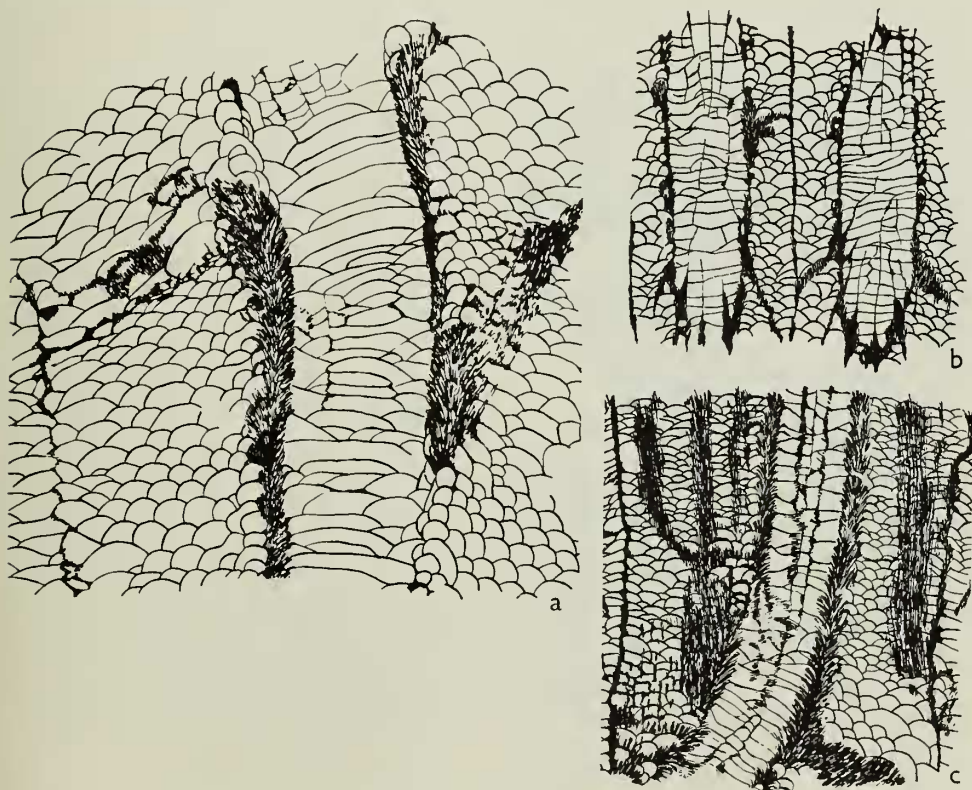


FIG. 3. Comparative longitudinal-sections: a. *Phillipsastrea hennahi hennahi* (OUM D520/p2); b. *Frechastraea pentagona pentagona* (OUM D537/p2); c. *Frechastraea carinata* (OUM D310b). All $\times 8$.

In the massive species described here, the septa are either more or less confluent between corallites (e.g. *Frecheastraea bowerbanki*) or intermingle to form a pseudotheca. The rôle of individual septa is usually clear in the formation of a diffuse and irregular pseudotheca such as that in the astraeoid *Phillipsastrea hennahi* (Text-fig. 4c). In some species of *Frecheastraea*, however, the peripheral ends of the septa are sharply geniculate and form a very strong wall by their fusion with one another (Text-fig. 4b). The part played by the individual septa is not clear although the septal characteristics of the pseudotheca are obvious. In *Frecheastraea carinata*, carinae may be rarely seen on the pseudotheca where the septal carination has been carried over into the wall. In the past, massive corals with such walls have been called cerioid (Rózkowska 1953 : 62) but this term should be strictly confined to massive corals in which an epitheca still surrounds individual corallites (Text-fig. 4a) (Lang 1923 : 123; Hill 1935 : 488). Thus the term “**pseudocerioid**” is introduced here to describe such corals as *Frecheastraea pentagona pentagona*, *F. carinata* and *F. goldfussi* in which a strong pseudotheca is built up by modified septal elements.¹

¹ See Addendum.

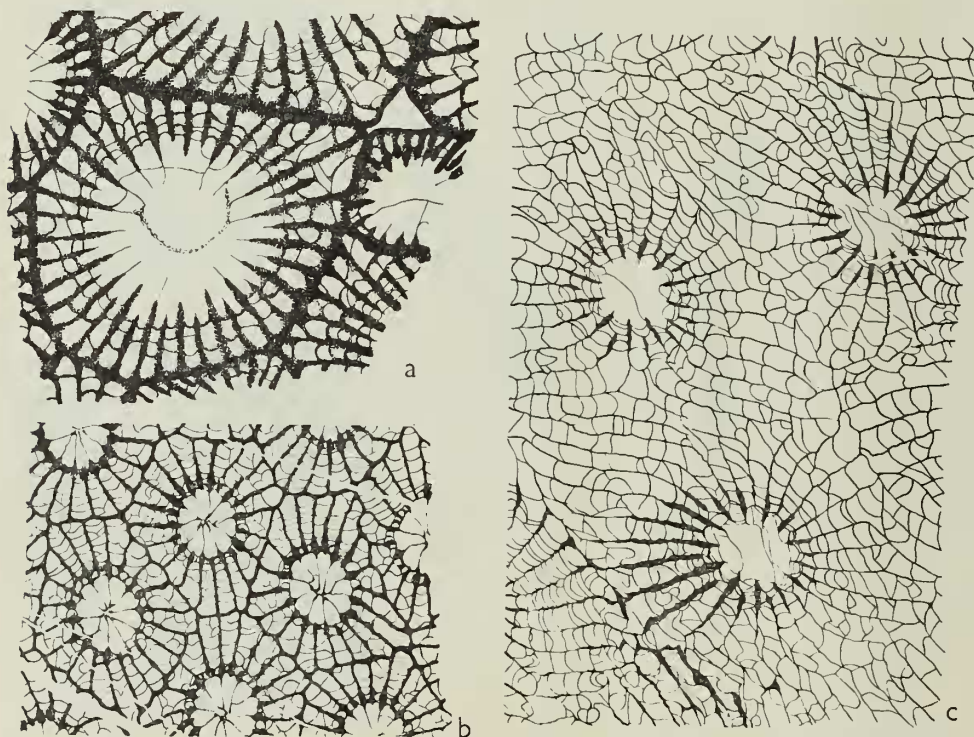


FIG. 4. Comparative wall structures: a. cerioid—*Hexagonaria firthi* (BM(NH) R29476); b. pseudocerioid—*Frecheastraea goldfussi* (OUM D539/p2); c. weak astraeoid—*Phillipsastrea hennahi hennahi* (OUM D520/p 1). All $\times 5$.

All the massive coralla described here are presumably surrounded by a holotheca (Hill 1935 : 497) although it has only been observed in *Frecheastraea micrommata* (C. F. Roemer) and in two sections of *F. goldfussi*. It is fibronormal in character and somewhat variable in thickness in the range 0.1–0.15 mm. Both the septa and the pseudotheca abut with a shallow convex surface against the holotheca, or penetrate slightly to form a wedge-shaped depression in its surface.

Thamnophyllum germanicum schoupppei, *T. caespitosum*, *T. caespitosum paucitubulatum* and *Peneckiella salternensis* have cylindrical corallites with fibronormal epithecae. The peripheral septal ends meet the epitheca and depress it slightly (Kato 1963, text-fig. 17f) in the same manner as the relationship between septa and holotheca in *F. goldfussi*.

In all cases where the microstructure can be distinguished, the tissue of dissepiments and tabulae is fibronormal.

(b) Increase.

For full details of corallum increase it is necessary to cut serial sections but in the present material, this has been possible only with *Thamnophyllum germanicum schoupppei*. Even in this subspecies, fracturing has so affected the point of branching that the details of septal insertion are obscured. Increase in the other taxa described here is known only from random sections cut through developing or immature individuals. Both axial and lateral increase are recorded and in some cases both may occur within the same colony.

At the present time no detailed work has been done on increase in plocoid rugose corals. Most of the methods of increase observed in the present material, however, have been briefly described by Rózkowska (1953). The most common process is the development of one or more new individuals in the border area of two or more surrounding adult corallites (Text-figs. 5a, b). Rózkowska (1953 : 39, 71) called

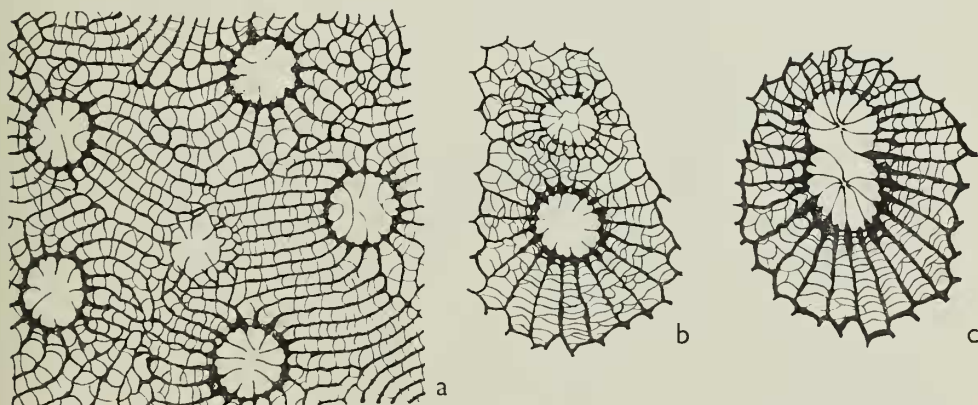


FIG. 5. Increase in massive Phillipsastraeidae: a. lateral (intercalicinal)—*Frecheastraea pentagona minima* (GSM PF4031); b. lateral—*Frecheastraea goldfussi* (BM(NH) R46370); c. axial—*Frecheastraea goldfussi* (BM(NH) R46370). 5a $\times 10$; 5b, c $\times 8$.

this "intermural" increase in the case of her "cerioid" colonies and "intercalicinal" increase in the forms she recognized as plocoid. In fact Rózkowska's use of cerioid is equivalent to the term pseudocerioid as used here, there being no epitheca but a pseudotheca, formed by modified septal ends separating individual corallites: these colonies are also, therefore, plocoid. Intermural increase was defined by Hill (1935 : 491) in terms of truly cerioid coralla and it was further restricted by Jull (1965 : 206) to daughter corallites which appear to develop between corallite walls without a particular parent. In view of the literal meaning of "intermural", Jull's definition is accepted here as it is within the original scope of the term and is most suitably described by it. Rózkowska's "intermural" increase (Rózkowska 1953 : 71 did mention that the term was not altogether appropriate) is better considered as a form of lateral increase. In some instances (Text-fig. 5b), the daughter corallite appears to develop in a very similar manner to that described as lateral in the cerioid *Lithostrotion* cf. *portlocki* by Jull (1965, text-fig. 6(1)). More usually in these pseudocerioid corals, however, the daughter corallite has no wall separating it from most, if not all, of the surrounding corallites during the early stages of development and the parent corallite may be very difficult to distinguish (see Rózkowska 1953, text-fig. 35). This latter situation seems not to differ fundamentally from intercalicinal increase in the other plocoid corals with weak or absent corallite walls (for example Text-fig. 5a and Rózkowska 1953, text-fig. 25). It is proposed, therefore, to term both the intermural and intercalicinal increase of Rózkowska (1953) as lateral increase. Full understanding of these processes in plocoid coralla, however, must await studies by serial sectioning.

Examples of axial increase have been seen much more rarely in the massive corals (Text-fig. 5c). Consequently, knowledge of the process is based on very few sections and cannot be described in full. Increase is apparently effected by the elongation and subsequent bilobation of the tabularium with commensurate insertion of new septa. The parent tabularium finally divides into two new individuals and their full rings of septa are completed in the area of fission. In all of the few examples seen there are never more than two new individuals formed at the same time.

Axial increase has been recorded in three massive species, all of which have predominant lateral increase (Table 1).

The process interpreted as "axial increase" by Rózkowska (1953 : 65, text-fig. 39) in her "*Phillipsastraea pentagona*" has also been observed in several specimens among the present material. From Rózkowska's figure and a consideration of the English specimens, however, it is doubtful whether this is really increase but rather a form of rejuvenescence in massive coralla. There is no indication that this phenomenon ever leads to the formation of two or more individuals. Confirmation of this interpretation must nevertheless await evidence from serial sectioning.

Mode of increase in the massive corals is summarized below (Table 1). It is possible that axial increase may be shown to occur in other species than those indicated when more material has been examined.

Of the phaceloid corals described here, one has exclusively axial increase and the others, exclusively lateral.

Thamnophyllum caespitosum and *Peneckiella salternensis* have a style of increase

TABLE 1.—Increase in massive *Phillipsastraeidae*.

	Lateral	Axial
<i>Phillipsastrea</i>		
<i>P. hennahi hennahi</i>	×	
<i>P. hennahi ussheri</i>	×	
<i>P. devoniensis</i>	No evidence	
<i>P. ananas</i>	×	¹
<i>P. rozkowskiae</i>	No evidence	
<i>Frechastreaea</i>		
<i>F. pentagona pentagona</i>	×	×
<i>F. pentagona minima</i>	×	×
<i>F. micrommata</i>	×	
<i>F. carinata</i>	×	×
<i>F. goldfussi</i>	×	×
<i>F. bowerbanki</i>	×	

¹ After Frech, 1885, pl. 2, fig. 5.

similar to that described as “thamnophylloid lateral” by Rózkowska (1960 : 31). The daughter corallite arises from the dissepimental tissue of the parent (Text-figs. 6, 7). In the early stages, the adult corallite becomes egg-shaped in cross-section with the more pointed end containing dissepimental tissue only, the septa having withdrawn from the epitheca in this area. This projection expands in size and septa begin to appear on the wall farthest from the parent. Some septa from the parent itself may extend slightly into the developing individual where the two are joined and these appear eventually to contribute to the latter's full complement of septa. As the process continues, the daughter corallite grows more circular and forms a bilobed complex with the parent. At the same time, new septa are inserted on

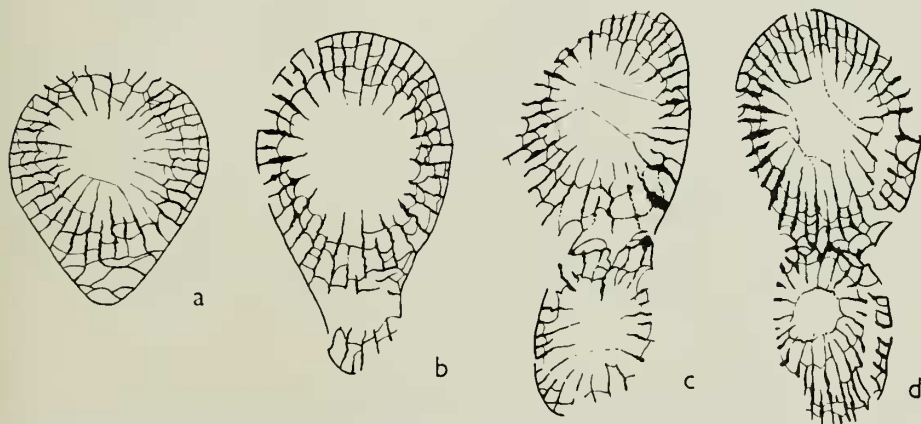


FIG. 6. Lateral increase in *Peneckiella salternensis*: a. OUM D553/p1; b. OUM D547/p1; c. OUM D547/p3 (same corallite as in 6b); d. OUM D553/p1. All $\times 5$.

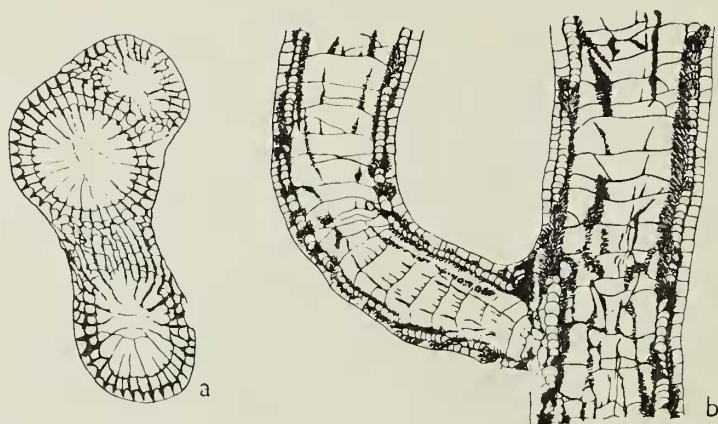


FIG. 7. Lateral increase in *Thamnophyllum caespitosum paucitubulatum*: a. BM(NH) R46162d; b. BM(NH) R46163d. Both $\times 3$.

both flanks of the daughter which now possesses most adult characteristics. During the bilobed stage, the two calices are wholly or partially separated by an irregular pseudotheca formed by the geniculation and mutual interference of the septa in the waist of the complex. The daughter corallite may be connected to the parent by extra-dissepimental tissue before final separation when the latter's epitheca may be complete. In *Thamnophyllum caespitosum* two daughter corallites may be produced at the same level but this has not been observed in *Peneckiella salternensis*.

Thamnophyllum germanicum schouppaei on the other hand displays exclusively axial increase similar to that found in many other species of *Thamnophyllum*. In all the specimens examined, either three or four daughter corallites are produced in each case. One specimen, in which increase is threefold, has been serial sectioned (Text-fig. 8). The parent corallite is about 5 mm. in diameter at the inception of increase which is marked by a striking change in skeletal deposition in the tabularium. After the last normal tabulae are laid down in the parent, the dissepimentarium continues to form as usual. In the tabularium, however, steeply inclined plates are secreted to form a cone (Text-fig. 8iii) which modifies upwards into a pyramid with as many sides as daughters are produced (Text-fig. 8iv, v). Upon these plates the new individuals are built up. As the cross-section of this axial structure changes in threefold increase from circular to triangular, three septa, each opposite and extending to join a corner of the triangle, become increasingly strongly developed. These delimit the areas of the new corallites. Thus each new corallite inherits roughly a third (or in fourfold increase, a quarter) of the mature septa and dissepiments of the adult. The first tabulae of each daughter are deposited between the base plate and the inherited dissepiments. Meanwhile the cross-section of the complex becomes increasingly trilobed (or tetralobed) and new septa are inserted along the inner margins of the developing corallites (Text-fig. 8vi, vii). The formation of the

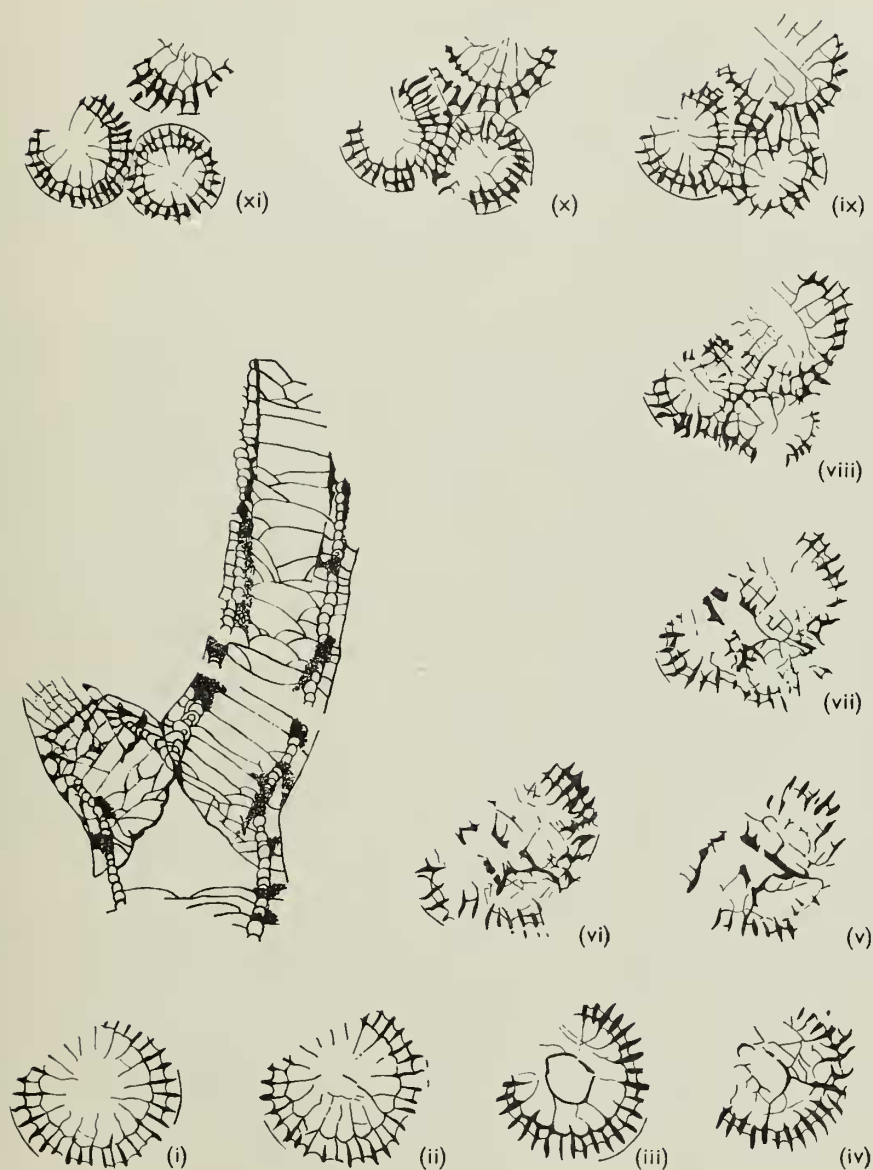


FIG. 8. Axial increase in *Thamnophyllum germanicum schouppei*: longitudinal-section after OUM D272; serial cross-sections after OUM D510/p5-10, p12-16. Spacing of sections in mm: i(p5)—0.747—ii(p6)—1.126—iii(p7)—0.712—iv(p8)—0.444—v(p9)—0.330—vi(p10)—0.533—vii(p12)—0.208—viii(p13)—0.267—ix(p14)—0.495—x(p15)—0.574—xi(p16). All $\times 5$.

new horizontal structural elements proceeds from the periphery towards the axial area of the complex and by the time the process is close to completion, vertical growth has passed the apex of the base plates and the daughters are in intimate contact (Text-fig. 8viii). Subsequently, the newly formed sections of the dissepimentaria acquire adult characteristics with distinct traces of horseshoe dissepiments in cross-section (Text-fig. 8ix, x) and the new corallites complete their epithecae. Evidently no extra-dissepimental tissue (caenogenetic tissue of Soshkina 1953) is formed in *Thamnophyllum germanicum schoupppei*, for as soon as the normal dissepimental tissue is developed, the daughters become phaceloid (Text-fig. 8xi).

(c) Variation.

(i) Introduction. Sufficient material is available of many of the taxa described here to allow their variation to be studied in some detail. The statistics are grouped with the individual species and subspecies as part of their characterization but their great interest is in the general trends they show which are commented upon here.

There are certain problems in the statistical treatment of south Devon material. Only one of the samples—*Thamnophyllum germanicum schoupppei* from Dyer's Quarry—is demonstrably from a population preserved more or less in position of growth. In all other cases the faunas from which collections have been made have apparently suffered some post-mortem movement, the extent of which is difficult to assess. The coral colonies are broken and disorientated, in most cases preserved in massive limestones which have suffered more or less from tectonic stresses and recrystallization.

The collections thus consist of fragmentary coralla which preclude ontogenetic study. The influence of ontogeny on the data obtained from these corals, however, appears to be small. Longitudinal-sections of corallites in the massive colonies show tabularium diameters to be virtually constant over most of their vertical growth. In this respect, they appear to behave in the same way as the phaceloid colonies, in which the influence of ontogeny is minimal in the extensive cylindrical parts of the corallites.

All measurements have been made in cross-sections. In many colonial corals, a large number of corallites are unavoidably cut at varying degrees of obliquity, resulting in elliptical sections. As the corallites in the phaceloid colonies and the tabularia in all the colonial corals considered here are circular in sections normal to their axes, diameter measurements have been made along the minor axis of the ellipse. Care has been taken to separate ellipticity due to oblique section from that resulting from crushing or tectonic distortion. Corallites which appear to have been deformed in this way have not been measured.

The following dimensions were recorded for each corallite:

- d** **corallite diameter.** Measured only in phaceloid colonies and recorded to the nearest 0.1 mm.
- dt** **tabularium diameter.** All of the corals described here have a clearly defined tabularium junction: recorded to the nearest 0.1 mm.
- n** **number of major septa.** Counts of the number of major septa were recorded with the corresponding **d** and/or **dt** value.

The following were calculated in the case of all massive coralla:

A **average corallite area in a colony.** As it is not possible to measure corallite diameter in a massive colony, the average corallite area in a colony was measured to facilitate comparison of corallite and tabularium size. Values of **A** were obtained by counting corallite numbers in a cross-sectional area measured by means of a transparent graticule divided into squares of 0.5 cm. side. The number of corallites was then divided into the corresponding area and the result recorded in square centimetres. Care was taken to calculate **A** from those corallites whose tabularia were also measured. This value is subject to some error due to the inclusion in its calculation of some obliquely sectioned corallites.

At **average tabularium area in a colony.** Calculated from $dt\bar{x}$ (the mean tabularium diameter) of each colony by the formula for the area of a circle and recorded in square centimetres.

From the above basic data, the following ratios were calculated:

dt/d **tabularium, corallite diameter ratio.** This ratio could only be calculated for phaceloid colonies.

n/d or n/dt **septal or septal-tabularium ratio** respectively. The septal ratio as normally applied to corals is the number of major septa divided by the corresponding corallite diameter, which in the present work could only be calculated for the phaceloid colonies. In the massive corals, the ratio of the number of major septa to the tabularium diameter, called the septal-tabularium ratio, was calculated. This ratio behaves in a similar way to the septal ratio but is not directly comparable with it. It will, of course, have higher values than corresponding septal ratios and may vary differently with size, depending on the variation in the dt/d ratio.

At/A **tabularium to corallite area ratio.** This ratio is the approximate counterpart in massive corals of the dt/d ratio in phaceloid corals. The **At/A** ratio, however, has only been calculated as an average for each colony and not for individual corallites because of the difficulty of measuring accurately the area of an irregularly polygonal corallite.

For the dimensions and ratios mentioned above, the following standard statistics were calculated:

N **sample size.** The number of corallites in the sample, with the number of colonies given in parentheses. In the case of **A**, **At**, and the ratio **At/A**, **N** is the number of colonies.

O.R. **overall range.**

$\bar{x}$ **mean value.**

s **standard deviation.**

C.V. **coefficient of variation.**

S.E._m **standard error of the mean.**

These elementary statistics are dealt with in many books and their application to zoology and palaeontology is discussed in Mayr, Linsley & Usinger (1953) and

Simpson, Roe & Lewontin (1960). Reference has been made to both these texts during the present work but principally, the writer has followed Imbrie (1956). The latter gives a clear and concise account of all the biometric techniques used here. It was found necessary, however, in view of the large size of most of the samples, to calculate the statistics for all characters except **A**, **At** and **At/A** by grouping the data in class intervals corresponding to the 0.1 mm. intervals in which the diameters were measured.

The statistics calculated for each species and subspecies and the representative colonies are given in tabular form with the systematic descriptions (Tables 4-16). The colonies selected for individual treatment were those in which the most corallites could be measured. Usually it was possible to use colonies with 50 or more corallites but in cases of species with large calices, smaller numbers had to be used. The colony with the least data is Colony 1 of *Thamnophyllum germanicum schoupppei* with 23 measured corallites.

The data are also illustrated graphically (Text-figs. 9-21). In the plots of **dt** against **d**, **n** against **d** or **dt**, **n/d** against **d** and **n/dt** against **dt**, diameter is recorded along the abscissa to the nearest 0.1 mm. As stated above, the character on the ordinate was averaged and plotted as a single point in each 0.1 mm. class. Thus points in the middle of the ranges of values on these graphs were based on many more observations than those at either end.

On all the graphs, the scatter of points approximated fairly closely to a straight line. When similar graphs are plotted for complete ontogenetic studies, it has been shown that the points usually fall on a curve of quite complicated form (see Voynovskiy-Kruger 1954). In the present case, however, the influence of ontogeny is thought to be slight and the data representative of the mature growth stages. Voynovskiy-Kruger's curves approximate very closely to straight lines in maturity (his "mature" plus "old" stages), as is shown by the present results. Thus straight lines have been calculated from the data represented by the scatter of points on each graph. For ease of comparison, the lines only are illustrated in the text-figures. After Imbrie (1956), the reduced major axis was chosen as the most suitable line for problems of relative growth.

For each line, the formula is given in the data tables as follows:

$$\left. \begin{array}{l} r \text{ correlation coefficient} \\ a \text{ "growth ratio"} \\ b \text{ "initial growth index"} \end{array} \right\} \text{line of the form } y = ax + b$$

Where statistical discrimination has been used between congeneric species and subspecies, the procedure followed is again that detailed by Imbrie (1956).

(ii) Variation in diameters. The assessment of size in these corals is mainly through the analysis of tabularium diameters as corallite diameters can only be measured in the phaceloid colonies. Variation in size may be the result of genetic, ontogenetic or ecological influences. Because of the parts played by the latter two factors, which are often not easy to assess, care must be taken in the significance placed on size differences and relative variation between colonies and species. In the present case, ecological control is largely an unknown factor although the influence of ontogeny may be regarded as minimal.

The variation in tabularium diameter in each of the taxa considered here is fairly similar (see Table 2). Values of C.V. range from 7.73 for the sample of *Frecheastraea bowerbanki* to 14.79 for the sample of *Thamnophyllum germanicum schoupppei*. Variation in the former, however, is almost certainly underestimated as only four incomplete colonies were available for measurement. Values of C.V. for the other species of *Frecheastraea* are all about 10. These figures are close to those obtained by Oliver (1960 : 83, table 7) for solitary cylindrical coral species and much lower than the variation he found in conical forms.

From the present data it is impossible to say if massive corals are more or less variable than phaceloid forms. Although *Thamnophyllum germanicum schoupppei* has the highest C.V. value, those for *T. caespitosum paucitabulatum* and *Peneckiella salternensis* are much the same as the values for many of the massive corals. In fact, the C.V. figure for the Barton Quarry sample of *Haplothechia pengellyi*, a massive marisastrid (see Scrutton 1967 : 274, table 2), is 15.75, which is higher than that for *T. germanicum schoupppei*. On the other hand, there is a general tendency for C.V. values to be higher with increase in mean tabularium diameter. In the phaceloid corals, variation in corallite diameters is roughly the same from species to species, although always lower, than in the corresponding tabularium diameters. Oliver's results with six solitary corals do not show such consistency and tabularium diameters are less variable than corallite diameters in two instances.

Variation in size within colonies, with only two exceptions, was found to be less than that in the total samples of the same species or subspecies from the same locality. One exception is Colony 1 of *Frecheastraea bowerbanki* (Table 12) which species has already been explained to be probably inadequately sampled. The other exception is Colony 1 of *Phillipsastrea hennahi hennahi* from Lummaton (Table 4). In this case, the C.V. value for *dt* in the colony only slightly exceeds that for the total Lummaton sample and is less than that for the sample from nearby Barton.

There is usually a considerable range in the C.V. values for colonies of the same species or subspecies, even when the number of measured corallites in each colony is the same or nearly so. This can be illustrated with reference to *Frecheastraea goldfussi* (Table 11) in which the C.V. values for 10 colonies range from 10.01 to 4.12, the value for the total sample from Ramsleigh Quarry being 10.10.

As coral colonies are ideally the result of asexual reproduction from one sexually produced individual, variation would be expected to be lower in a single colony than in a sample of several colonies. From the results obtained here this is generally substantiated. The wide range in colonial variability may be due in part to several factors. Microenvironmental and general ecological influences undoubtedly exercise some control on variation but their effects cannot be easily assessed. In the case of phaceloid colonies, high C.V. values may be the result of the intergrowth of two or more colonies which have been sampled as one. As Oliver (1960 : 74) pointed out, it is virtually impossible to detect intergrowth when collecting material, and this may well have been responsible for the high C.V. values in the colonies of *Thamnophyllum germanicum schoupppei* (Table 13). Another factor for consideration is the fusion of several sexually produced polyps at an early stage of colony formation,

TABLE 2.—Comparative means and coefficients of variation for all characters and taxa analysed. Species and subspecies are arranged in order of increasing $dt\bar{x}$. *F.* = *Frechastraea*; *Ph.* = *Phillipsastrea*; *T.* = *Thamnophyllum*; *P.* = *Penectiella*.

d	$\bar{x}$ C.V.	<i>F.</i> <i>pentagona</i> minima	<i>F.</i> <i>carinata</i>	<i>F.</i> <i>pentagona</i>	<i>F.</i> <i>goldfussi</i>	<i>F.</i> <i>bowyerbairdi</i>	<i>Ph.</i> <i>hemnahi</i> usshevi	<i>Ph.</i> <i>hemnahi</i> (Lumm.)	<i>Ph.</i> <i>hemnahi</i> (Bar.)	<i>T.</i> <i>germanicum</i> schoupsbei	<i>P.</i> <i>salternensis</i>	<i>T.</i> <i>caespitosum</i> paucicubulatum
dt	$\bar{x}$ C.V.	0.96 10.98	1.02 10.56	1.09 9.38	1.53 10.10	1.54 7.73	2.04 10.61	2.32 10.13	2.45 13.27	2.69 14.79	3.51 10.87	3.70 10.88
n	$\bar{x}$ C.V.	9.54 4.42	9.75 3.51	10.12 3.15	11.16 4.57	9.54 2.59	12.46 3.07	12.67 2.89	12.92 3.22	16.52 7.41	19.91 4.21	18.92 3.95
n/d	$\bar{x}$ C.V.									3.98 7.51	3.80 7.34	3.35 8.78
n/dt	$\bar{x}$ C.V.	10.05 6.40	9.66 7.07	9.36 6.34	7.32 5.80	6.24 5.48	6.16 8.97	5.52 8.16	5.25 11.69			
dt/d	$\bar{x}$ C.V.									0.64 2.43	0.67 1.68	0.65 3.27
At/A	$\bar{x}$ C.V.	0.062 12.21	0.063 17.68	0.079 18.63	0.10 17.74	0.054 6.13	0.063 26.12	0.042 17.31	0.045 23.41			

recorded in Recent corals by Stephenson (1931 : 124). The effect of this phenomenon would generally be to increase the variation displayed by the colony.

It is very difficult to separate the effects due to these different factors but it seems likely from the wide range in C.V. values shown, for example, by the colonies of *F. goldfussi*, that primary polyp fusion could be an important factor.

The investigation of colonial variation described here differs from that made by Oliver (1960 : 73 *et seq.*) through the latter comparing septal ratio C.V. values for individual colonies with those for populations of solitary cylindrical corals. In addition, Oliver analysed the total sample of *Tryplasma fascicularia* from colony means rather than the basic corallite data.

(iii) Variation in septal number and the septal ratios. With the exception of *Thamnophyllum germanicum schoupppei*, the C.V. values for septal number are very similar in all the total samples. There appears to be no relationship between the degree of variation and the mean septal number (Table 2).

It has long been known that septal number depends to some extent on calice size. When one is plotted against the other for both colonies and total samples, *n* shows a general increase with increasing *d* or *dt* in every case. Correlation coefficients in the total samples are usually about 0.9. The figure in individual colonies is slightly lower but much the same from colony to colony. Only rarely does the correlation coefficient drop below 0.7. These figures reflect the strength of the linear relationship between *n* and *d* or *dt* in mature individuals. A correlation between septal number and diameter is still reflected to a large extent in Table 2 as taxa with larger mean diameters have, with few exceptions, greater mean values for *n*.

This relationship had led to the use of the septal ratio (septal coefficient of Voynovskiy-Kruger 1954) as a useful diagnostic criterion in coral species. Rózkowska (1957) particularly, has used a form of this ratio, her *Ms*, in a detailed statistical study of species of *Thamnophyllum* and *Macgeea* from Poland. She showed (p. 91 and Table 6) that successively younger species and subspecies of *Thamnophyllum* have lower *Ms* values and similarly, fewer septa at a given diameter. A comparison of Rózkowska's figures with the *thamnophyllids* described here is shown in Table 3.

It can be seen that the *n* values at *d* = 6 mm. for the English material follow the same trend as for the Polish specimens but do not fit exactly into the latter's scale. On the other hand, the English *Ms* values (the English data has been recalculated for direct comparison with Rózkowska's figures) are quite different from their approximate age equivalents in Poland and do not fit into a stratigraphical trend. It is interesting, however, to arrange the same taxa in order to increasing mean corallite diameter. This produces a series of decreasing *Ms* values somewhat less perfect than before for the Polish specimens but into which the English figures fit quite well. The values of *n*, however, show somewhat less perfect ordering than when arranged in stratigraphical series.

Turning to the massive corals in Table 2, the mean *n/dt* figures for the representatives of *Frecheastraea* and *Phillipsastrea* show a perfect series of decreasing values with increasing mean tabularium diameter. Furthermore, just such correlation exists, this time between mean *d* and mean *n/d*, in the corals described by Oliver

TABLE 3.—Series in **Ms** and **n** (at **d** = 6 mm.) for English (E) and Polish (P) *thamnophyllids*. Polish figures from Rózkowska (1957 : 91 and table 6).

	Horizon	Name	Country	Ms	n (at d =6 mm.)
Frasnian	Middle	<i>T. superius</i>	P	2.20	15
	Lower	<i>T. kozlowskii</i>	P	2.30	17
Givetian	Upper	<i>T. caespitosum paucitabulatum</i>	E	3.50	19.35
	Middle	<i>T. caespitosum caespitosum</i>	P	3.17	20
		(<i>T. germanicum pajchela</i>)	P	(3.60)	(21)
		<i>T. caespitosum</i>	E	3.15	20
		<i>T. germanicum germanicum</i>	P	3.42	21
		<i>T. germanicum skalense</i>	P	3.64	22
		<i>T. germanicum schoupppei</i>	E	4.16	20.28

	$\bar{x}$ d				
	4.11	<i>T. germanicum pajchela</i>	P	3.60	21
	4.14	<i>T. germanicum schoupppei</i>	E	4.16	20.28
	5.36	<i>T. germanicum skalense</i>	P	3.64	22
	5.68	<i>T. caespitosum paucitabulatum</i>	E	3.50	19.35
(ca.)	6.00	<i>T. caespitosum caespitosum</i>	P	3.17	20
	6.17	<i>T. caespitosum</i>	E	3.15	20
	7.00	<i>T. germanicum germanicum</i>	P	3.42	21
	9.28	<i>T. superius</i>	P	2.20	15
	10.03	<i>T. kozlowskii</i>	P	2.30	17

(1960). Thus the correlation between mean size and mean septal ratio is quite strong. The stratigraphical series in **Ms** values obtained by Rózkowska may simply reflect the tendency in her material for larger species and subspecies of *Thamnophyllum* to occur at higher horizons.

Between conspecific colonies, the septal or septal-tabularium ratio behaves in the same way. Colonies with greater mean diameters have, with very few exceptions, smaller values for the mean septal ratio.

This trend is related to the fact that the septal ratio is not constant throughout ontogeny but decreases in value (see Voynovskiy-Kruger 1954) with increasing corallite diameter. When septal ratio is plotted against diameter, the relationship is more or less linear for mature corallites. In the present case correlation coefficients for the total samples range between -0.90 and -0.94 for phaceloid and -0.96 and -1.0 for massive corals.

C.V. values for septal number and the septal or septal-tabularium ratio in conspecific colonies may show a considerable range. Furthermore, the relative variation in these characters and **d** or **dt** between colonies is usually different, although there is a slight tendency for the colony with the highest **C.V.** value for diameter to have high **C.V.** values for septal number and the septal ratio as well (see for example

Table 11). In the case of **n**, the **C.V.** value reflects to some extent the rate of septal insertion as well as the amount of variation in diameter, and this masks any independent variation in the septal number. Colonies with similar variation in diameter, for example, show a strong correlation between **a**, the growth ratio, in graphs plotting **n** against **d** or **dt** and **C.V.** values for **n**. Similarly, **C.V.** values for **n/d** or **n/dt** in conspecific colonies also correlate roughly with values of **a** for graphs plotting **n/d** or **n/dt** against **d** or **dt**, and inversely with values of **a** for the plots of **n** against **d** or **dt**.

(iv) Variation in size ratios. In the phaceloid forms, tabularium diameter increases evenly with increase in corallite diameter. The relationship between the two is strongly linear, reflected in the high values for the correlation coefficient ($r > 0.95$ in all cases). Only three phaceloid colonies have been analysed individually, those of *Thamnophyllum germanicum schoupppei*. Their correlation lines on the graph plotting **dt** against **d** are virtually superimposed (Text-fig. 20).

The ratios of tabularium to corallite diameter have very low **C.V.** values, partially reflecting the fact that they are virtually unaffected by changes in diameter. Measurements are confined, however, to mature corallites. Oliver (1960 : 71) has shown that during ontogeny in *Siphonophrentis variabilis* and *Pseudoblothrophyllum helderbergium*, this ratio decreases with increasing diameter. In his analyses of mature individuals, on the other hand, the ratio remains relatively constant with increasing diameter, as is shown in the present material.

The relationship between tabularium and corallite size in massive corals is considered in terms of their respective areas and is restricted to total samples. Analyses of **A**, **At**, and the **At/A** ratio show these characters to have high **C.V.** values. In the same sample there may be a considerable difference between the **C.V.** value for **A** and that for **At**, for example in the case of *Phillipsastrea hennahi ussheri* in which the former figure is more than double the latter (Table 5). This is undoubtedly due in part to the difficulty in calculating accurately the value of **A**. In most cases, however, the two figures are more nearly comparable.

When **At** is plotted against **A**, there is always a clear tendency for the former to increase with increase in the latter (Text-figs. 12, 19). The scatter of points, however, is considerable and is reflected in the low values for the correlation coefficient. Calculations using the formulae for the fitted lines show that the **At/A** ratio may increase or decrease slightly with increasing corallite area. Thus the analyses suggest that this ratio behaves similarly, if not so regularly, as the **dt/d** ratio and is largely independent of size in mature colonies.

V. SYSTEMATIC DESCRIPTIONS

The family name Phillipsastraeidae was erected by Roemer (1883 : 389) to include the genera *Phillipsastrea* and *Pachyphyllum*. It has, however, been little used until recently and taxonomists have usually classified the nominal type genus in the Disphyllidae. Hill (1939 : 224) erected the Disphyllidae to include both the typical *Disphyllum* and the related *Prismatophyllum* (considered by Lang, Smith & Thomas 1940 : 104 as a junior synonym of *Hexagonaria*) as well as *Phillipsastrea* (interpreted by Hill 1939 : 236 to contain species both with and without horseshoe

dissepiments) and the exclusively horseshoe bearing genera, *Thamnophyllum*, *Macgeea* and *Trapezophyllum*. Hill's concept of the Disphyllidae was largely influenced by Lang & Smith's (1935) discussion of these genera.

Many subsequent workers followed Hill's combination of horseshoe and non-horseshoe bearing forms in the same family. Stumm (1949 : 31) extended the range of genera included in the Disphyllidae but divided them among three subfamilies, the Pachyphyllinae, Disphyllinae and Eridophyllinae, characterised respectively by the presence and absence of horseshoe dissepiments and the development of an aulos. He considered *Phillipsastrea* to lack horseshoe dissepiments and placed it with *Disphyllum*, *Hexagonaria* and *Billingsastraea* in the Disphyllinae. The Pachyphyllinae included *Pachyphyllum*, *Macgeea*, *Thamnophyllum* and *Trapezophyllum*.

Soshkina (1949), on the other hand, distributed the genera and species here included in the Phillipsastraeidae among three new families on the basis of morphological and ontogenetic considerations. Genera she considered to develop horseshoe dissepiments and a "hexacoralloid" microstructure—*Pachyphyllum*, *Macgeea*, *Thamnophyllum* and *Synaptophyllum*—Soshkina (1949 : 76) grouped in the Thamnophyllidae, equivalent to Stumm's Pachyphyllinae. She placed *Phillipsastrea*, erroneously quoting (1951 : 95) *P. radiata* as type species and interpreting the genus as lacking horseshoe dissepiments, with *Neocolumnaria* and *Schluteria* in the Neocolumnariidae (1949 : 145). The third new family, the Peneckelliidae (1949 : 141) included *Peneckella* and *Megaphyllum*. The latter was considered by Hill (1956 : 280) to be a synonym of *Disphyllum*.

Soshkina (1951, 1952, 1954) continued to use this classification with the introduction of further genera to the latter two families and (1954 : 44) replacing the name Neocolumnariidae by Neocampophyllidae. Spassky (1960) followed Soshkina's (1954) classification.

Wang (1950 : 217) further enlarged the Disphyllidae by incorporating the acanthophyllids into the family. He based his classification on a consideration of coral microstructure, defining the family chiefly on the development of one or more fan systems in the septal trabeculae. Wang's use of the subfamily Phacellophyllinae (septal trabeculae with a marked area of divergence) corresponds very closely to the scope of the Phillipsastraeidae as interpreted herein. Like Lang & Smith (1935) and Hill (1939), however, he included species both with and without horseshoe dissepiments in *Phillipsastrea*.

Rózkowska (1953 : 8 *et seq.*) considered the three different classifications of Stumm (1949), Wang (1950) and Soshkina (1951). She decided that coral microstructure was of particular diagnostic importance and for this reason followed Wang's classification in principle. She did, however, remove the Acanthophyllinae from the Disphyllidae. In addition, she used the subfamily Pachphyllinae *sensu* Stumm in preference to the Phacellophyllinae *sensu* Wang as the former was conceived as exclusive of the genus *Phillipsastrea*. This genus Rózkowska interpreted as lacking horseshoe dissepiments and placed in the subfamily Disphyllinae.

Hill (1954a, b) reintroduced the family name Phillipsastreidae (*sic*) effectively as a senior synonym of her (1939 : 224) Disphyllidae. Although the 1954 papers contain no familial diagnosis, this classification was later given in full by Hill

(1956 : 179). She considered *Phillipsastrea* to lack horseshoe dissepiments and thus placed all the genera with disphyllid and marisastrid dissepimentaria in the Phillipsastreaeinae, and the horseshoe bearing genera in the Phacellophyllinae.

Schouppé (1956) discussed at length the classifications of previous authors. He stressed the importance of the so-called "hexacoralloid" microstructure developed in these corals with strongly reflexed dissepimentaria, and advocated their clear systematic separation. Two years later, Schouppé (1958) published a classification on this basis, stressing at the same time the presence of horseshoe dissepiments in the lectotype of *Phillipsastrea hennahi*. He placed all the genera with an area of divergence in their septal trabeculae, usually but not always associated with horseshoe dissepiments, in the Phillipsastreaeacea (*sic.*). Thus he elevated what had previously been a family or even a subfamily concept to the level of a suborder.

Schouppé subdivided the Phillipsastreaeacea into the Macgeeiidae, with subfamilies Macgeeiinae and Peneckellinae, and the Phillipsastreaeidae. He placed the genera *Phillipsastrea* and *Billingsastrea* together in the Phillipsastreaeidae and listed (1958 : 233) the family characteristics as massive astreaoid form, with a pseudotheca and never an epitheca between adjacent corallites, and with a broad dissepimentarium often developing horseshoe dissepiments. *Phillipsastrea* and *Billingsastrea*, however, are not considered to be closely related (Oliver 1964 : 2; Scrutton 1967 : 276). Furthermore, Schouppé placed *Haplothechia* Frech, *Pachyphyllum sensu* Rózkowska (1953) and *Pseudoacervularia sensu* Rózkowska (1953) in his synonymy for *Phillipsastrea*, all of which include species with a partial or complete epitheca around some or all corallites. The Macgeeiidae *sensu* Schouppé, on the other hand, was defined by the presence of horseshoe and usually also flat dissepiments in a narrow dissepimentarium, with an epitheca surrounding individual corallites. All the genera included in this family by Schouppé, with the exception of *Synaptophyllum*, belong to the Phillipsastreaeidae as defined herein.

Rózkowska (1957 : 82) rejected her earlier classification in favour of that proposed by Soshkina (1949) to the extent of placing all horseshoe dissepimentate genera in the Thamnophyllidae. Rózkowska referred to Schouppé's (1956 : 151) views but decided to separate those forms with horseshoe dissepiments from those without among the group with trabecular fans. Rózkowska (1965 : 261), however, accepted almost completely Schouppé's (1958) classification and erected a new family, the Marisastridae, for Phillipsastreaeacea with an epitheca but no horseshoe dissepiments (see Scrutton 1967).

On the other hand, Strusz (1965) rejected Schouppé's (1958) familial and ordinal groupings, placing all genera with horseshoe dissepiments in the Phacellophyllidae. Genera with trabecular fans but no horseshoe dissepiments he included in the Disphyllidae. Strusz (1965 : 523) drew attention to a distinction between forms with "half fans" and full "disphylloid fans" within this family but placed no particular taxonomic significance upon it.

The confused classification of this group of corals reflects the difficulty of distinguishing clear phylogenetic relationships between the genera involved. Morphology is extremely variable, particularly in massive forms, and results in general gradations between the characters considered diagnostic of different family and sub-

family groups. A particular feature of more recent classifications resulting from this is the uncertainty in placing corals lacking horseshoe dissepiments but having a fan shaped arrangement of the septal trabeculae. Schouppé (1958) grouped them with the horseshoe bearing forms whilst Strusz (1965) grouped them with the disphyllids *sensu stricto*. All workers are agreed, however, that horseshoe dissepiments and the related trabecular fans must be considered of particular importance in taxonomy. Horseshoe dissepiments are unique to this group of Devonian corals and great stress has been laid, particularly by Soshkina (1949), Schouppé (1956) and Rózkowska (1957) on the development of a pseudo-hexacoralloid trabecular pattern.

The trabecular arrangement alone, however, has, in the writer's opinion, been somewhat overstressed and does not justify the rank of suborder *sensu* Schouppé (1958). On the other hand, the development of specialized dissepimental types (horseshoe and peneckielloid dissepiments), with their related trabecular structure, defines with relative clarity a group of corals whose general morphological characteristics support a close family relationship. This group includes the genus *Phillipsastrea* (as defined herein) and should be classified as the Phillipsastraeidae. The writer does not agree with Strusz (1965 : 524) concerning the use of this family name. It must be noted that the generic name *Phillipsastrea* has been used far more often in a disphyllid sense than the corresponding family name. The genus, however, should not be suppressed simply because its type species has been imperfectly known in the past and in this case, the change in concept of the family name will naturally follow that of the genus.

The genera with reflexed dissepimentaria lacking horseshoe or peneckielloid dissepiments but possessing an open fan shaped arrangement of the trabeculae form a group of their own, intermediate in character between the Phillipsastraeidae as defined herein and the disphyllids *sensu stricto*. This is formalized in the family Marisastridae *sensu* Scrutton (1967). Finally, the Disphyllidae is here restricted to forms in which the trabeculae are arranged in half fans, or in a sub-parallel sense throughout on non-reflexed dissepimentaria. This family, in the writer's opinion, should be interpreted to conform strictly to the dissepimental pattern of the type genus *Disphyllum*.

Family PHILLIPSASTRAEIDAE Roemer 1883

- 1883 Phillipsastraeidae Roemer 389.
- partim* 1922 Campophyllidae Wedekind 3.
- partim* 1929 Pexiphyllidae Walther 117.
- partim* 1939 Campophyllidae; Soshkina : 12.
- partim* 1939 Cyathophyllidae; Sanford : 408.
- partim* 1939 Disphyllidae Hill 224.
- partim* 1940 Disphyllidae; Hill : 258.
- partim* 1942c Disphyllidae; Hill : 186.
- partim* 1949 Disphyllidae; Stumm : 31.
- partim* 1949 Thamnophyllidae Soshkina : 76.
- partim* 1949 Peneckiellidae Soshkina : 141.
- partim* 1949 Neocolumnariidae Soshkina : 145.
- partim* 1950 Disphyllidae; Wang : 217.
- partim* 1951 Disphyllidae; Taylor : 183.

- partim* 1952 Disphyllidae; Lecompte : 470.
partim 1953 Disphyllidae; Rózkowska : 9.
partim 1954a Phillipsastreidae; Hill : 14.
partim 1954b Phillipsastreidae; Hill : 107.
partim 1955 Columnariidae; Glinski : 86.
partim 1956 Phillipsastraeidae; Hill : 279.
 1957 Thamnophyllidae; Rózkowska : 83.
partim 1958 Macgeeiidae; Schouppé : 218.
partim 1958 Phillipsastraeidae; Schouppé : 232.
partim 1959 Disphyllidae; Middleton : 152.
partim 1959 Phillipsastraeidae; McLaren : 22.
partim 1960 Thamnophyllidae; Spassky : 44.
partim 1961 Phillipsastraeidae; Semenov-Tian-Chansky : 294.
 1962 Thamnophyllidae; Soshkina : 308.
partim 1962 Disphyllidae; Soshkina & Dobrolubova : 334.
partim 1962 Phillipsastraeidae; Soshkina & Dobrolubova : 336.
 1964 Phacellophyllidae; Pedder : 366.
 1965 Phacellophyllidae; Strusz : 554.
 1966 Phacellophyllidae; Pedder : 183.

TYPE GENUS. *Phillipsastrea* d'Orbigny 1849 : 12.

DIAGNOSIS. Solitary, dendroid, phaceloid or massive rugose corals. Septa of two orders, major and minor, more or less dilated at the tabularium boundary which is usually sharply defined. Characterized by an area of divergence in the septal trabeculae centred on a complete or incomplete series of horseshoe dissepiments, peneckielloid dissepiments or a series of highly globose dissepiments occasionally modified to a horseshoe form.

DISTRIBUTION. Lower and particularly Middle and Upper Devonian of Europe, Asia, Australia and North America.

DISCUSSION. Of the genera assigned to this family, all but two have a more or less well developed series of horseshoe dissepiments. The exceptions are *Peneckiella* and *Frechastrea* gen. nov.

Peneckiella may show considerable variation in dissepimental form but is characterized by the development of peneckielloid dissepiments. Frequently these are accompanied by sigmoidal, horseshoe and flat dissepiments in varying proportions. Rózkowska (1960 : 32, 48, 50) who named the *Peneckiella* dissepimental types considered them to be the breakdown products of a typical *Thamnophyllum* dissepimentarium, and that *Peneckiella* evolved from this genus.

The species and subspecies of *Frechastrea* develop rare horseshoe dissepiments against the tabularium junction. This genus is thought to have evolved from *Phillipsastrea* principally through the gradual loss of horseshoe dissepiments and thus should be classified with the Phillipsastraeidae.

The full list of genera here included in the Phillipsastraeidae is as follows:

Phillipsastrea d'Orbigny 1849 (Synonyms *Smithia*, *Pachyphyllum*, *Medusae-phyllum*, ?*Streptastrea*, *Pseudoacervularia* and ?*Keriophylloides*).

Macgeea Webster 1889 (Synonyms *Pexiphyllum* and *Protomacgeea*).

Thamnophyllum Penecke 1894 (Synonym *Phacellophyllum*).

Trapezophyllum Etheridge 1899.

Peneckiella Soshkina 1939 (Synonyms *Acinophyllum* and *Sudetia*).

Sulcorphyllum Pedder 1964.

Bensonastrea Pedder 1966.

Frechastraea gen. nov. (see p. 231).

Synaptophyllum Simpson 1900 was long considered to develop horseshoe dissepiments and to belong to this group of corals. McLaren (1959), however, has shown that this genus had been wrongly used due to the misinterpretation of the type species.

The genera fall roughly into two groups. *Phillipsastrea*, *Sulcorphyllum*, *Bensonastrea* and *Frechastraea* usually have several rows of normal dissepiments as well as the modified ones, whilst *Macgeea*, *Thamnophyllum*, *Peneckiella* and *Trapezophyllum* commonly have only two series of dissepiments, one horseshoe or peneckielloid and the other usually flat. Both Schouppé (1958) and Rózkowska (1965) regarded the presence (in the second group) or absence of an epitheca between corallites as an additional criterion when they advocated a division at the family level along these lines. Rózkowska has particularly stressed wall structure as important in familial classification.

Unfortunately, there are several exceptions to this grouping which mitigate against even subfamily status. Species of *Phillipsastrea* are known which have an epitheca around some corallites (Scrutton 1967 : 266) whilst a toptype of *Trapezophyllum elegantulum* (B.M. (N.H.) R46001) is pseudoceroid at least in part. The number of rows of dissepiments can be very variable in some species of *Thamnophyllum* (for example *T. soshkinae* (Rózkowska)) and *Frechastraea* (for example *F. goldfussi* (de Verneuil & Haime)). Further, a classification based on dissepimental rows would place *Sulcorphyllum* in a different group to *Trapezophyllum* whereas the two genera appear to be closely related. Thus it is preferred not to recognize subfamily divisions in the Phillipsastreaidae.

Genus *PHILLIPSASTREA* d'Orbigny 1849

- 1849 *Phillipsastrea* d'Orbigny : 12.
- partim* 1850 *Lithostrotion*; d'Orbigny : 106.
- partim* 1850 *Favastrea*; d'Orbigny : 107.
- partim* 1850 *Actinocyathus*; d'Orbigny : 107.
- partim* 1850 *Phillipsastrea*; d'Orbigny : 107.
- 1850 *Pachyphyllum* Edwards & Haime : 68.
- partim* 1850 *Acervularia*; Edwards & Haime : 70.
- 1850 *Phillipsastrea*; Edwards & Haime : 70.
- 1851 *Pachyphyllum*; Edwards & Haime : 168, 396.
- partim* 1851 *Acervularia*; Edwards & Haime : 414 (*non* 171).
- partim* 1851 *Smithia* Edwards & Haime : 171, 421.
- partim* 1851 *Syringophyllum*; Edwards & Haime : 449 (*non* 173).
- 1851 *Arachnophyllum*; M'Coy : 72.
- 1853 *Pachyphyllum*; Edwards & Haime : 234.
- partim* 1853 *Acervularia*; Edwards & Haime : 236.
- partim* 1853 *Smithia*; Edwards & Haime : 240.
- 1853 *Syringophyllum*; Edwards & Haime : 242.
- partim* 1855 *Acervularia*; F. A. Roemer : 30.

- 1855 *Medusaephyllum* F. A. Roemer : 33.
 1855 *Smithia*; F. A. Roemer : 33.
 ? 1856 *Streptastrea* Sandberger & Sandberger : 416.
 1881 *Pseudoacervularia* Schlüter : 84.
partim 1883 *Phillipsastraea*; C. F. Roemer : 389.
partim 1883 *Pachyphyllum*; C. F. Roemer : 392.
partim 1885 *Phillipsastrea*; Frech : 44.
 1885 *Phillipsastrea* (*Pachyphyllum*); Frech : 65.
partim 1889 *Phillipsastraea*; Schafer : 398.
partim 1896 *Phillipsastrea*; Gürich : 178.
 1896 *Pachyphyllum*; Gürich : 181.
 1909 *Smithia*; Gürich : 102.
 1917 *Phillipsastraea*; Smith : 284.
 1935 *Pachyphyllum*; Lang & Smith : 554.
partim 1935 *Phillipsastraea*; Lang & Smith : 556.
partim 1939 *Phillipsastraea*; Hill : 236.
 1940 *Medusaephyllum*; Lang, Smith & Thomas : 83.
 1940 *Pachyphyllum*; Lang, Smith & Thomas : 92.
 1940 *Phillipsastraea*; Lang, Smith & Thomas : 99.
 1940 *Pseudoacervularia*; Lang, Smith & Thomas : 108.
 ? 1940 *Streptastrea*; Lang, Smith & Thomas : 125.
partim 1942a *Phillipsastrea*; Hill : 153.
partim 1942b *Phillipsastrea*; Hill : 186.
 1942c *Phillipsastrea*; Hill : 186.
partim 1945 *Phillipsastraea*; Smith : 36.
partim 1949 *Phillipsastraea*; Stumm : 34.
 1949 *Pachyphyllum*; Stumm : 37.
partim 1950 *Phillipsastraea*; Wang : 220.
 1951 *Phillipsastrea*; Taylor : 192.
 1951 *Pachyphyllum*; Taylor : 193.
 1951 *Pachyphyllum*; Soshkina : 84.
 ? 1951 *Keriophylloides* Soshkina : 102.
partim 1952 *Pachyphyllum*; Soshkina : 86.
partim 1952 *Phillipsastraea*; Lecompte : 471.
 1953 *Pachyphyllum*; Rózkowska : 39.
 1953 *Pseudoacervularia*; Rózkowska : 49.
partim 1954a *Phillipsastrea*; Hill : 14.
 ? 1954b *Phillipsastrea*; Hill : 107.
 1954 *Pachyphyllum*; Soshkina : 68.
 1956 *Pachyphyllum*; Rózkowska : 317.
partim 1956 *Phillipsastrea*; Hill : 280.
 1956 *Pachyphyllum*; Hill : 282.
partim 1958 *Phillipsastraea*; Schouppé : 233.
 1958 *Pachyphyllum*; Bulvanker : 89.
partim 1959 *Phillipsastraea*; Middleton : 156.
 1961 *Pachyphyllum*; Semenoff-Tian-Chansky : 303.
partim 1962 *Phillipsastraea*; Soshkina & Dobrolubova : 336.
 1964 *Phillipsastraea*; Fontaine : 84.
 1965 *Phillipsastrea*; Strusz : 564.

But not:

- 1819 *Acervularia* Schweigger : tab. 6.
 1828 *Lithostrotion* Fleming : 508.
 1846 *Arachnophyllum* Dana : 186.

- 1849 *Actinocyathus* d'Orbigny : 12.
- 1850 *Syringophyllum* Edwards & Haime : 72.
- 1851 *Phillipsastrea*; Edwards & Haime : 173, 447.
- 1852 *Phillipsastrea*; Edwards & Haime : 203.
- 1855 *Syringophyllum*; Edwards & Haime : 295.
- 1951 *Phillipsastrea*; Soshkina : 95.
- 1952 *Phillipsastrea*; Soshkina : 101.
- 1953 *Phillipsastrea*; Rózkowska : 57.
- 1954 *Phillipsastrea*; Soshkina : 45.
- 1958 *Phillipsastrea*; Bulvanker : 118.
- 1960 *Phillipsastrea*; Spassky : 65.

DIAGNOSIS. Cerioid, pseudocerioid, astraeoid, thamnasterioid, aphroid or rarely secondarily phaceloid, rugose corals. Major and minor septa with spindle-shaped dilatation at tabularium boundary. In dissepimentarium, a series of horseshoe dissepiments is well developed at or near junction with tabularium; several series of normal dissepiments also present. Tabulae complete or incomplete.

TYPE SPECIES. (Selected by Edwards & Haime 1850 : 71). *Astrea hennahii* Lonsdale (1840 : 697, pl. 58, figs. 3, 3^b, non fig. 3a) = *Astraea hennahii* Lonsdale; Phillips (1841 : 12, pl. 6, figs. 162a, 162b, 162c, non pl. 7, fig. 15D): upper Givetian limestones; Barton Quarry, Torquay.

DISTRIBUTION. Middle and Upper Devonian of Europe and Asia. Lower and Middle Devonian of Australia. Upper Devonian of North America.

DISCUSSION. *Phillipsastrea* was erected by d'Orbigny (1849 : 12) who quoted as examples of the genus "*Astrea parallela* et *hennahii* Phillips". In the following year he redefined the genus (1850 : 107), spelling it this time *Phillipsastrea* and splitting up the specimens illustrated by Lonsdale (1840) and Phillips (1841) as *A. hennahi* among the genera *Phillipsastrea*, *Lithostrotion* and *Actinocyathus*. D'Orbigny's original spelling *Phillipsastrea* is employed here following Hill (1956 : 279) who considered the spelling *Phillipsastrea* to be a *nomen vanum*.

The confusion created by Edwards & Haime (1850 : 70; 1851 : 173) who quoted first "*Astrea hennahi* Lonsdale" and later *Erismatolithus Madreporites radiatus* Martin (1809, pl. 18) as type species of *Phillipsastrea* has been clearly documented by Smith (1917 : 284). He showed the selection of *A. hennahi* to be valid and placed *Phillipsastrea radiata* and other Carboniferous species assigned to *Phillipsastrea* in the genera *Aulina* and *Orionastrea*.

Edwards & Haime's invalid designation however was still accepted by Russian workers up to the beginning of this decade (see Soshkina 1954 : 45; Bulvanker 1958 : 118; Spassky 1960 : 65) and Soshkina (1952 : 86) described *A. hennahi* Lonsdale as a species of *Pachyphyllum*. More recently, however, Soshkina & Dobrolubova (1962 : 336) have assigned the correct type species to *Phillipsastrea*.

Various authors in the last century, particularly Edwards & Haime, assigned a number of Devonian colonial corals to *Acervularia* Schweigger. In fact, Edwards & Haime (1850 : 70) unwarrantably cite *Acervularia roemeri* de Verneuil & Haime as type species of that genus. *Acervularia*, however, the type species, by monotypy, of which is *Madrepora ananas* Linnaeus 1758 : 797 = *Acervularia baltica* Schweigger

1819, Table 6; Upper Silurian, Gotland, Sweden, is typically Silurian with only a superficial resemblance to the Devonian forms. With the closer study of internal structures in later years, the Devonian species of *Acervularia* were removed from that genus and usually reassigned to *Phillipsastrea* (see Frech 1885 : 44). Schlüter (1881 : 84) had, in fact, erected a new genus *Pseudoacervularia* expressly to cover the Devonian "acervulariids", but this genus has been little used. Indeed, a type species was not selected until Lang, Smith & Thomas (1940 : 108) chose *Acervularia coronata* Edwards & Haime for that purpose. Unfortunately the type specimens of *A. coronata* are missing but the species is almost certainly conspecific with *Phillipsastrea hennahi*, and *Pseudoacervularia* is a subjective synonym of *Phillipsastrea*.

Rózkowska (1953 : 39), apparently unaware of Lang, Smith & Thomas' selection, invalidly chose *Acervularia macrommata* F. A. Roemer as type species of *Pseudoacervularia*. She described several species of that genus, all of which should be placed in *Phillipsastrea*.

A most critical factor in the taxonomic position and interpretation of *Phillipsastrea* has been the emphasis placed by Schouppé (1958 : 156) on the development of horseshoe dissepiments in the lectotype of the type species. Hitherto, the presence of these specialized dissepiments in the lectotype had not been widely realized and the genus had been either restricted to species lacking horseshoe dissepiments (Stumm 1949 : 34; Rózkowska 1953 : 57; Hill 1956 : 280), or considered to include species both with and without horseshoe dissepiments (Lang & Smith 1935 : 556; Hill 1939 : 236; Smith 1945 : 36). In addition, Edwards & Haime (1850 : 68) had erected the genus *Pachyphyllum* with *P. bouchardi* as type species. The latter has long been known to develop horseshoe dissepiments and many authors (Stumm 1949 : 37; Soshkina 1951 : 84; Rózkowska 1953 : 39) have used the genus specifically for Middle and Upper Devonian massive phillipsastreids with well developed horseshoe dissepiments.

Schouppé (1958 : 233 *et seq.*), however, placed *Pachyphyllum* in synonymy with *Phillipsastrea*. At the same time, he removed all the forms previously assigned to the latter genus which he thought to lack horseshoe dissepiments and placed them in *Billingsastraea* Grabau (see comments under that genus by Scrutton (1967 : 276) and under *Frechastraea* gen. nov. herein).

The writer agrees with Schouppé's concept of *Phillipsastrea* with the exception of the placing of *Haplothechia* Frech. Schouppé (1958 : 201) claimed that the type species of the latter developed horseshoe dissepiments. However, an examination of the lectotype of *H. filata* (Schlotheim), type species of *Haplothechia*, does not substantiate this (Scrutton 1967 : 271) and the genus is here regarded as quite distinct from *Phillipsastrea*.

Semenoff-Tian-Chansky (1961 : 303) was not convinced that *Phillipsastrea* and *Pachyphyllum* should be considered congeneric and he mentioned two particular points of apparent difference in overall size and dissepimental arrangement. With regard to the considerable disparity in size between the respective type species, the existence of species of intermediate size must not be overlooked—for example *Phillipsastrea ananas* (Goldfuss), *P. devoniensis* (Edwards & Haime), *P. ibergensis* (F. A. Roemer) and *P. chenouensis* (Semenoff-Tian-Chansky). In fact it would

appear that, quite fortuitously, *Phillipsastrea hennahi* is one of the smallest and *Pachyphyllum bouchardi* the largest of the species assigned to *Phillipsastrea*. The apparent discrepancy between *Pachyphyllum* and *Phillipsastrea* in the arrangement of the normal dissepiments was based on a comparison with Schouppé's (1958, text-fig. 21; pl. 5, fig. 1) longitudinal illustrations of *P. hennahi*. As remarked elsewhere, although purporting to come from the lectotype, they are completely different from longitudinal slides, and peels taken from that specimen by the writer, which are illustrated here (Pl. 1, figs. 2-4, 6). There is in fact no basic difference in the dissepimental arrangement between *P. hennahi* and *P. bouchardi*.

Phillipsastrea is thus interpreted as including all those Devonian massive corals, excepting species of *Trapezophyllum*, *Sulcorphyllum* and *Bensonastrea*, in which a series of horseshoe dissepiments is well developed in the dissepimentarium. *Trapezophyllum* Etheridge (1899 : 32) differs from *Phillipsastrea* in possessing only one row of flat dissepiments peripheral to the horseshoe series and in this respect is related more closely to *Thamnophyllum*. *Sulcorphyllum* Pedder (1964 : 366) is like *Trapezophyllum* but with several rows of normal dissepiments separating the peripheral flat dissepiments from the horseshoes adjacent to the tabularium. The irregular, incomplete tabulae of this genus are unlike those found in European phillipsastreids. *Sulcorphyllum* is, for the present, considered distinct from *Phillipsastrea* but a better knowledge of the variation in the former may require its taxonomic position to be reconsidered in the future. *Bensonastrea* Pedder (1966 : 183) is distinguished by its vepreculate and peripherally degenerate septa, and complex dissepimentarium.

Phillipsastrea hennahi hennahi (Lonsdale)

Plate 1, figs. 1-6; Plate 2, figs. 1-4

- 1840 *Astrea* (*Siderastrea*) *hennahii* Lonsdale : 697 *pars*, pl. 58, figs. 3, 3b (*non* 3a).
- 1841 *Astraea hennahii* Lonsdale; Phillips : 12 *pars*, pl. 6, figs. 16αa, 16βb, 16βc (*non* pl. 7, fig. 15D).
- 1841 *Astraea intercellulosa* Phillips : 12, pl. 6, fig. 17.
- ? 1843 *Astraea hennahii* Lonsdale; F. A. Roemer : 5, pl. 2, fig. 13.
- 1849 *Phillipsastrea hennahii* (Phillips) d'Orbigny : 12 *pars*.
- 1850 *Lithostrotion hennahii* (Lonsdale) d'Orbigny : 106.
- 1850 *Favastraea intercellulosa* (Phillips) d'Orbigny : 107.
- 1850 *Actinocyathus hennahii* (Phillips) d'Orbigny : 107.
- 1850 *Phillipsastraea hennahii* (Phillips); d'Orbigny : 107 *pars*.
- ? 1850 *Acervularia roemeri* de Verneuil & Haime : 162.
- 1850 *Phillipsastrea cantabrica* de Verneuil & Haime : 162 (*nomen nudum*).
- 1850 *Phillipsastrea hennahi* (Lonsdale); Edwards & Haime : 71 *pars*.
- 1851 *Acervularia coronata* Edwards & Haime : 416.
- ? 1851 *Acervularia roemeri* de Verneuil & Haime; Edwards & Haime : 420.
- 1851 *Smithia hennahii* (Lonsdale) Edwards & Haime : 421.
- 1851 *Syringophyllum*? *cantabricum* (de Verneuil & Haime) Edwards & Haime : 451.
- 1851 *Arachnophyllum hennahi* (Lonsdale) M'Coy : 72.
- 1853 *Acervularia coronata* Edwards & Haime; Edwards & Haime : 237, pl. 53, figs. 4a-b (2fig. 4).
- 1853 *Acervularia roemeri* de Verneuil & Haime; Edwards & Haime : 239, pl. 54, figs. 3, 3a.
- 1853 *Smithia hennahii* (Lonsdale); Edwards & Haime : 240, pl. 54, figs. 4-4d.

- 1853 *Syringophyllum cantabricum* (de Verneuil & Haime); Edwards & Haime : 242, pl. 55, figs. 3-3a.
 ? 1855 *Smithia hennahi* (Phillips); F. A. Roemer : 33, pl. 6, fig. 25.
 ? 1856 *Streptastrea longiradiata* Sandberger & Sandberger : 416, pl. 37, figs. 3-3b.
 ? 1879 *Acervularia roemeri* de Verneuil & Haime; Quenstedt : 535, pl. 162, fig. 38.
 1879 *Astrea hennahii* Lonsdale; Quenstedt : 535.
 1883 *Acervularia coronata* Edwards & Haime; C. F. Roemer : 352.
 ? 1883 *Acervularia roemeri* de Verneuil & Haime; C. F. Roemer : 353.
 1883 *Phillipsastraea hennahii* (Lonsdale); C. F. Roemer : 390.
 1885 *Phillipsastrea roemeri* (de Verneuil & Haime) Frech : 57 *pars*, pl. 4, ? fig. 2 (*non* figs. 1, 3-5).
 1885 *Phillipsastrea hennahi* (Lonsdale); Frech : 59 *pars*, pl. 5, fig. 1, (*non* figs. 2-4).
 1917 *Phillipsastraea hennahi* (Lonsdale); Smith : 284, pl. 22, figs. 1-4.
 1945 *Phillipsastraea hennahi* (Lonsdale); Smith : 37, pl. 19, figs. 1a, b.
 1952 *Pachyphyllum hennahi* (Lonsdale) Soshkina : 86.
 1958 *Phillipsastraea hennahi* (Lonsdale); Schouppé : 235, ?text-figs. 20, 21, ?pl. 5, fig. 1.
 1959 *Phillipsastraea hennahi* (Lonsdale); Middleton : 156.
 1963 *Phillipsastraea hennahi* (Lonsdale); Fontaine : 84, pl. 8, figs. 5, 6.

But not:

- 1953 *Pseudoacervularia roemeri* (de Verneuil & Haime) Rózkowska: 53, text-figs. 27, 28, pl. 7, figs. 3, 4.

DIAGNOSIS. Astraeoid tending to thamnasterioid *Phillipsastrea*. Mean tabularium diameter 2.45 mm. with 10 to 16 major septa (topotype sample). Septa thin peripherally, with a variable spindle-shaped thickening at tabularium junction. Dissepimentarium composed of several rows of normal dissepiments with a single series of horseshoe dissepiments developed against tabularium. Tabulae complete or incomplete, usually in form of wide flat plates with downturned edges. Increase lateral.

LECTOTYPE. Selected by Edwards & Haime (1851: 421). The original of Lonsdale's (1840, pl. 58) figures 3 and 3b which is GSM (Geol. Soc. Coll.) 6185; upper Givetian limestones; Barton Quarry, Torquay.

MATERIAL. Barton Quarry: OUM D514 (Colony 1), OUM D306 (Colony 2), OUM D512 (Colony 3), BM(NH) R5615 (Colony 4). Other measured specimens: GSM (Geol. Soc. Coll.) 6185 (lectotype), OUM D515-6, OUM D518-20, OUM D522, TM(JB) 107-8, TM(JB) 120. Additional material: OUM D240 (= D282), OUM D513, OUM D517, OUM D523, TM(JB) 139.

Lummaton Quarry: TM(JB) 61 (Colony 1), TM(JB) 59 (Colony 2), BM(NH) R23484 (Colony 3). Other measured specimens: TM(JB) 63-4, TM(JB) 78-9. Additional material: TM(JB) 62, TM(JB) 69.

Wolborough Quarry: OUM D521.

Babbacombe Cliff: BM(NH) R46176.

Dartington Hall: GVM13/1, GVM14/2.

Torquay, South Devon: OUM D74 (holotype, *Astraea intercellulosa* Phillips), GSM (Geol. Soc. Coll.) 6189 (lectotype here chosen, *Syringophyllum cantabricum* Edwards & Haime).

DISTRIBUTION. England: upper Givetian limestones of Barton and Lummaton quarries, Torquay; middle Givetian limestones of Wolborough Quarry, Newton Abbot; Givetian limestones, 100 ft. above sea level, south end Babbacombe cliffs, Torquay; middle Givetian limestones of Dartington Hall area (Middleton 1959); Middle Devonian, Plymouth (Phillips 1841). Devonian, Kikai, Yunnan (Fontaine 1963). Also represented in the Frasnian, Ibergerkalk, Bad Grund, Harz, Germany (Frech 1885). Middle Devonian, Pola de Gordon, León, Spain (de Verneuil & Haime 1850).

DESCRIPTION. All specimens are incomplete and details of the colony exterior, its overall size and shape are unknown. The largest specimen examined was, when complete, 17×14 cm. in surface area and 5 cm. deep (it is now in two pieces numbered separately as OUM D240 and OUM D282).

Colonies are astraeoid tending to thamnasterioid, with a straight or zigzagged pseudotheca of variable strength separating the corallites. This pseudotheca may break down round parts of the corallite margins when the septa run more or less confluent from one corallite to the next.

The septa, major and minor, are very thin peripherally, less than 0.1 mm. and normally about 0.025 mm. in thickness. They may have smooth or slightly roughened sides and rarely some separation of the trabeculae but they are never truly carinate. They are usually sinuous, seldom straight, in the dissepimentarium and occasionally curved in a constant direction to form a vortex. The septa develop a spindle-shaped dilatation in the region of the tabularium junction. It is extremely variable both within colonies and individual corallites, ranging normally between 0.15 and 0.25 mm. width and 1 to 2 mm. length (see, for example TM(JB)79, Pl. 2, fig. 1).

Within the tabularium, the major septa usually taper smoothly and end somewhat short of the axis of the corallite. Occasionally, however, some may reach the axis, or cross the tabularium periaxially to join with major septa in the adjacent quadrant of the corallite. Rarely the axial ends of the major septa may develop slight lobate thickenings. The minor septa do not enter the tabularium.

Dissepiments are usually uniserial but may occasionally be multiserial between adjacent septa. In cross-section they are well spaced peripherally, becoming more crowded towards the tabularium junction which is sharply defined. Against this junction, the trace of a single series of horseshoe dissepiments is sometimes clearly seen (Pl. 2, fig. 2 corallite in right centre).

In longitudinal-section, the dissepimentarium is composed of several rows of small, normal dissepiments, between 0.2 and 0.5 mm. in height. They are weakly arched peripherally but become increasingly globose towards the tabularium boundary. The dissepiments immediately adjacent to the tabularium are modified into horseshoe form resulting in a single vertical series of more or less well developed horseshoe dissepiments (Pl. 1, figs. 2-6). The surface of the dissepimentarium slopes downwards away from this series and flattens out peripherally.

The tabulae are complete or incomplete, more usually the latter. In general they are strikingly flat and parallel across the axis of the tabularium, usually with downturned peripheral edges. There is a limited development of vesicular, periaxial

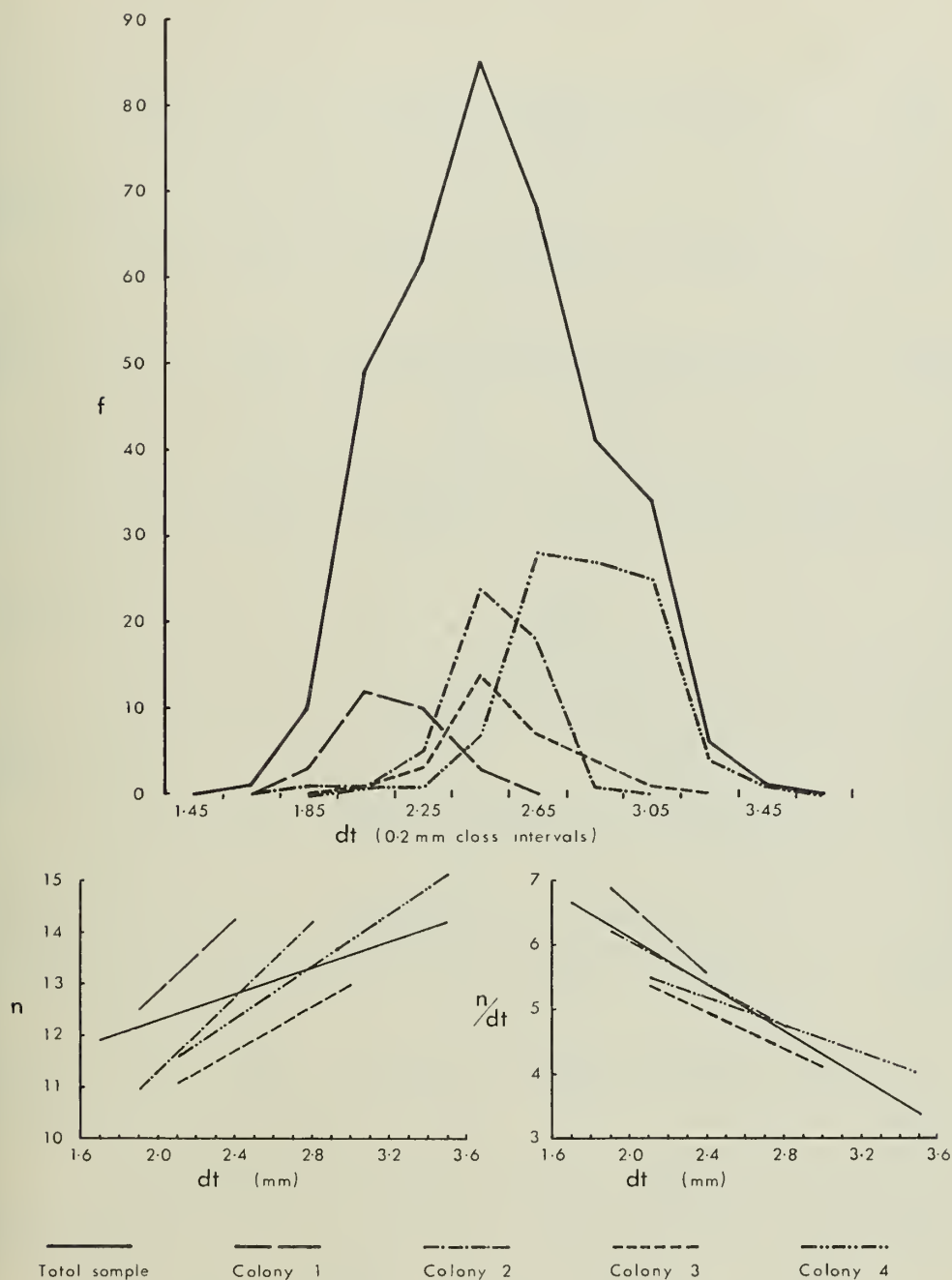
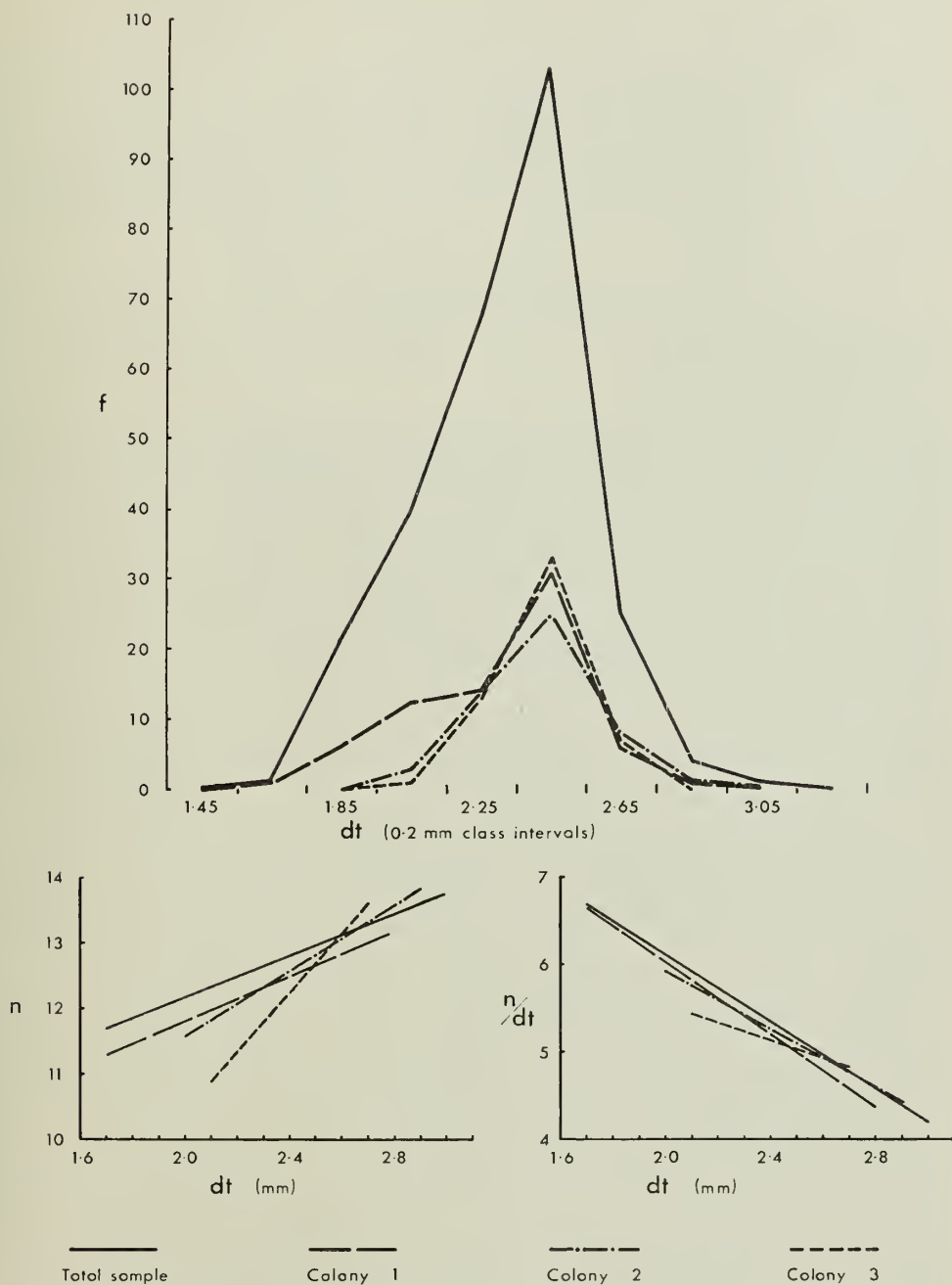
FIG. 9. *Phillipastrea hennahi hennahi* (Barton sample).

TABLE 4.a. Statistical data for some characters of *Phillipsastrea hennahi* (Barton sample). b. Statistical data for some characters of *Phillipsastrea hennahi* (Lunmaton sample).

(a)									
	Total sample	Colony 1	Colony 2	Colony 3	Colony 4	Total sample	Colony 1	Colony 2	Colony 3
N	357 (14)	28	50	30	94	261 (7)	71	51	54
O.R.	1.7-3.5	1.9-2.4	1.9-2.8	2.1-3.0	2.1-3.5	1.7-3.0	1.7-2.8	2.0-2.9	2.1-2.7
$\bar{x}$	2.45	2.14	2.49	2.55	2.82	2.32	2.31	2.40	2.43
s	0.33	0.16	0.17	0.21	0.23	0.24	0.24	0.17	0.12
C.V.	13.27	7.23	6.75	8.09	8.07	10.13	10.58	6.95	5.05
S.E. _m	0.018	0.029	0.024	0.038	0.024	0.015	0.029	0.023	0.17
O.R.	10-16	12-14	12-15	11-13	11-15	10-15	10-14	11-14	10-14
$\bar{x}$	12.92	13.36	13.08	12.03	13.40	12.67	12.34	12.57	12.39
s	0.42	0.55	0.60	0.43	0.57	0.37	0.41	0.41	0.55
C.V.	3.22	4.08	4.61	3.61	4.21	2.89	3.24	3.27	4.46
S.E. _m	0.022	0.10	0.085	0.079	0.058	0.023	0.049	0.058	0.075
O.R.	3.79-7.37	5.42-7.00	4.62-6.32	4.14-5.72	3.93-5.72	4.23-7.78	4.23-7.37	4.44-6.50	4.58-6.08
$\bar{x}$	5.25	6.28	5.26	4.74	4.77	5.52	5.40	5.26	5.09
s	0.61	0.41	0.28	0.29	0.24	0.45	0.50	0.28	0.12
C.V.	11.69	6.47	5.30	6.16	4.94	8.16	9.29	5.29	2.39
S.E. _m	0.033	0.077	0.039	0.053	0.024	0.028	0.060	0.039	0.017
Graphs:—									
r	0.70	0.42	0.73	0.75	0.89	0.88	0.70	0.69	0.89
n/dt a	1.26	3.53	3.59	2.10	2.48	1.56	1.69	2.46	4.49
b	9.78	5.83	4.14	6.67	6.41	9.07	8.44	6.66	1.46
n/dt /	-0.96	-0.83	-0.75	-0.89	-0.91	-0.98	-0.95	-0.88	-0.45
a	-1.85	-2.63	-1.65	-1.41	-1.03	-1.92	-2.06	-1.67	-0.99
b	9.87	11.90	9.38	8.35	7.69	9.96	10.14	9.26	7.50
(b)									
						A	At	At/A	Graph:—At/A
O.R.	0.86-1.54	0.034-0.065	0.035-0.074	Graph:—At/A		O.R.	0.68-1.35	0.032-0.047	0.034-0.053
$\bar{x}$	1.08	0.046	0.045	r	0.78	$\bar{x}$	1.01	0.041	0.042
s	0.20	0.011	0.010	a	0.055	s	0.25	0.0061	0.0072
C.V.	18.70	23.84	23.41	b	-0.013	C.V.	24.94	14.94	17.31
S.E. _m	0.054	0.0030	0.0028			S.E. _m	0.095	0.0023	0.0027

FIG. 10. *Phillipsastrea hennahi hennahi* (Lummaton sample).

elements. Tabularium structure varies in complexity from the simple, interleaved tabulae of TM(JB) 79 (Pl. 1, fig. 5) to the close spaced series of flat-topped domes in GSM (Geol. Soc. Coll.) 6185 (Pl. 1, figs. 2-4, 6).

Despite the large number of specimens examined, only one instance of lateral increase has been seen and that is in the lectotype.

Statistical analyses have been made of samples of this subspecies from the type locality, Barton Quarry (14 colonies) and Lummaton Quarry (7 colonies), both in Torquay. Four colonies from Barton and three from Lummaton have been analysed individually. The statistics are given in Table 4 and illustrated graphically in Text-figs. 9, 10 and 12.

The topotypes are characterized by a mean tabularium diameter of 2.45 mm. with 10 to 16 major septa and a mean septal-tabularium ratio of 5.25. The Lummaton specimens differ principally in having a smaller overall range and mean *dt*, and a somewhat larger mean *n/dt*.

Colonial variation at the two localities displays an interesting contrast. Generally there is a greater range in the mean values of the quantitative characters between the colonies from Barton, although variation within each colony is much the same. The Lummaton colonies, on the other hand, have very similar mean values but markedly different degrees of variation from colony to colony.

DISCUSSION. The specimen on which Phillips (1841 : 12) erected *Astraea intercellulosa* is OUM D74 (Pl. 2, figs. 2, 3). Phillips himself had great doubts as to whether or not his specimen was distinct from Lonsdale's species. In the writer's opinion it is an atypical representative of *P. hennahi hennahi* in which the septa are virtually unthickened.

F. A. Roemer (1843 : 5, pl. 2, fig. 13) described and figured as *Astraea hennahi* Lonsdale a specimen which was later selected by de Verneuil & Haime (1850 : 162) as the type of a new species *Acervularia roemeri*. The identity of Roemer's original is uncertain but Edwards & Haime (1853 : 239, pl. 54, figs. 3, 3a) later recorded *A. roemeri* from Torquay. The latter's specimen, judging from their figures, is almost certainly consubspecific with *P. hennahi hennahi*. Frech (1885, pl. 4, figs. 1-5) also figured *Phillipsastrea roemeri* (de Verneuil & Haime), of which, if his interpretation was correct, the original of his fig. 2 is a topotype. Again it appears from the illustration that the specimen may be consubspecific with *Phillipsastrea hennahi hennahi*.

Edwards & Haime (1853) described and figured two species, *Acervularia coronata* and *Syringophyllum cantabricum*, previously erected by them in 1851 (p. 416 and p. 451 respectively). In the case of *A. coronata*, Edwards & Haime's original material has been lost or mislaid. From their illustrations (1853, pl. 53, figs. 4a, b) of a specimen from Barton, however, the species is almost certainly the same as the present subspecies. "*Phillipsastrea cantabrica* n. sp." in de Verneuil & Haime (1850 : 162) is a *nomen nudum* as they give neither description nor figures of the species. Edward & Haime (1851 : 451) must therefore be regarded as the authors of the species with their description of "*Syringophyllum? cantabricum* (de Verneuil & Haime)". The original of Edwards & Haime's (1853, pl. 55, figs. 3, 3a) figures of *Syringophyllum cantabricum* is specimen GSM (Geol. Soc. Coll.) 6189, which is here

chosen as lectotype of the species (Pl. 2, fig. 4). This specimen is consubspecific with *P. hennahi hennahi*.

Schouppé (1958, text-fig. 21, pl. 5, fig. 1) published two illustrations which he stated were taken from a longitudinal peel of specimen GSM (Geol. Soc. Coll.) 6185. The structure of both the tabularium and the dissepimentarium in Schouppé's figures, however, is not that seen in this specimen although the presence of horseshoe dissepiments can be confirmed. The source of Schouppé's figures must thus be considered somewhat enigmatic.

Phillipsastrea hennahi ussheri subsp. nov.

Plate 3, figs. 1-3

DERIVATION OF NAME. The subspecies is named after W. A. E. Ussher (1849-1920).

DIAGNOSIS. Astraeoid tending to thamnasterioid *Phillipsastrea*. Mean tabularium diameter 2.04 mm. with 10 to 14 major septa (topotype sample). Septa thin peripherally but usually strongly dilated at tabularium junction, becoming laterally contiguous and forming a dense inner wall. Horseshoe dissepiments developed in a series adjacent to tabularium with several rows of normal dissepiments peripherally. Tabulae usually incomplete with narrow axial series of flat topped domes irregularly developed. Increase lateral.

HOLOTYPE. OUM D544. Lower Frasnian limestones; road cutting, 20 yd. west of the entrance to Ramsleigh Quarry, East Oghwell, near Newton Abbot.

MATERIAL. Ramsleigh Quarry: BM(NH) R23402 (Colony 1), BM(NH) R5616 (Colony 2), BM(NH) R23209 (Colony 3).

Road cutting, 40 yd. west of Ramsleigh Quarry entrance. Measured specimens: OUM D533-4.

Road cutting, 20 yd. west of Ramsleigh Quarry entrance. OUM D545.

DISTRIBUTION. Lower Frasnian limestones in and around Ramsleigh Quarry.

DESCRIPTION. Only incomplete colonies have been found and the overall colony shape, size and external features are unknown.

The colonies are astraeoid tending to thamnasterioid with considerable variation in the strength of the pseudotheca. Perfectly confluent septa between adjacent corallites, however, are rare. Septa are thin peripherally, usually about 0.06 mm. thick, occasionally straight but more usually sinuous. The sides of the septa may be smooth or slightly crenulate; carinae are not developed. Immediately adjacent to the tabularium, the septa are dilated. The short, spindle-shaped thickening is greater on the major septa when it is usually 0.5 to 0.7 mm. long and about 0.25 mm. wide. The dilatation is a very constant feature, frequently bringing adjacent septa into contact to form a dense wall, about 0.5 mm. wide, round the tabularium. Minor septa end at the tabularium junction but the major septa thin abruptly and continue as very fine filaments, about 0.02 mm. thick, towards the axis of the corallite. Sometimes the ends of the major septa, slightly withdrawn from the axis, bear small lobate thickenings which through lateral contact may form a pseudoaulos. In

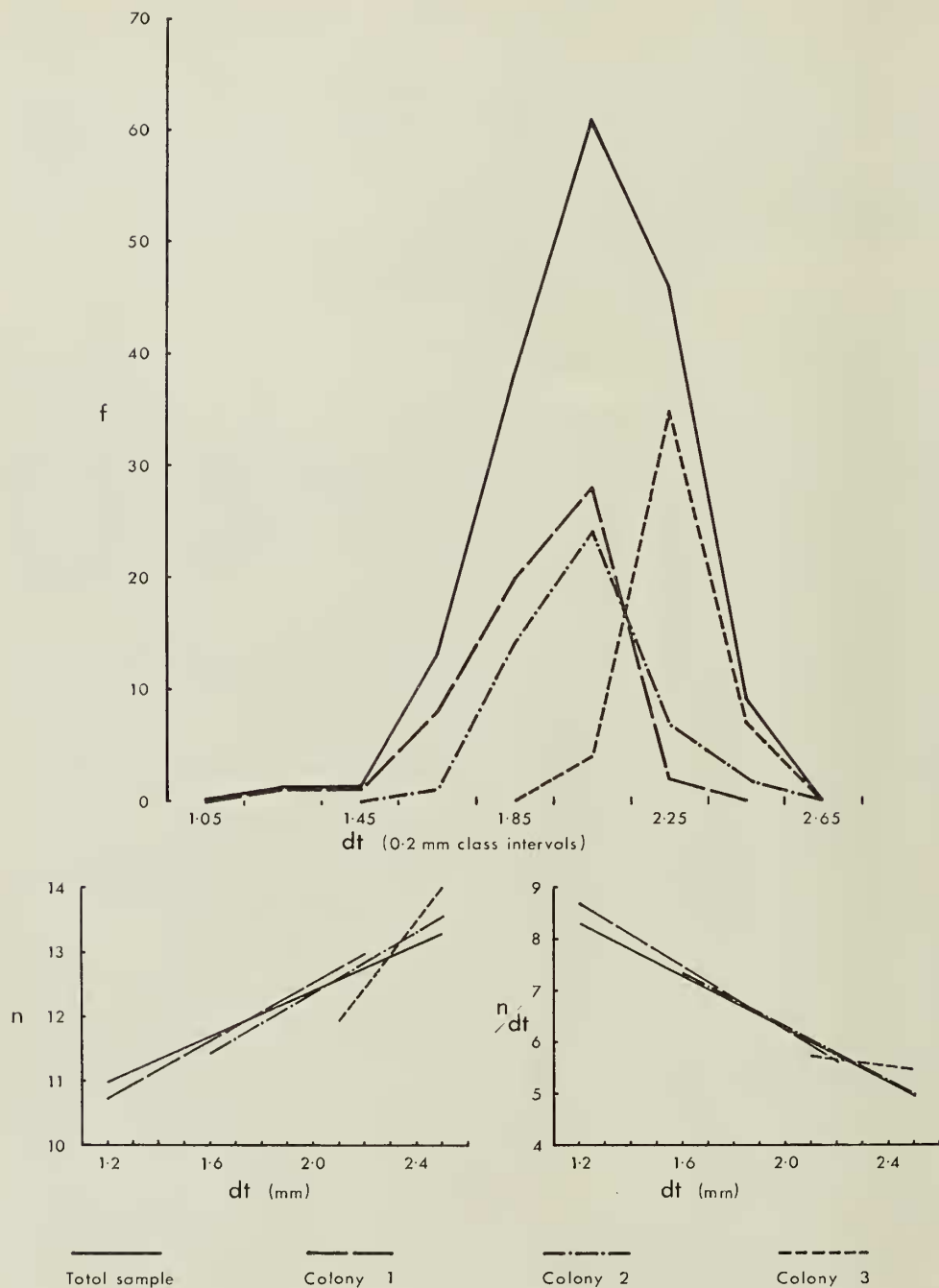
FIG. 11. *Phillipsastrea hennahi ussheri*.

TABLE 5.—Statistical data for some characters of *Phillipsastrea hennahi ussheri*.

		Total sample	Colony 1	Colony 2	Colony 3
	N	169 (5)	60	48	46
dt	O.R.	1.2-2.5	1.2-2.2	1.6-2.5	2.1-2.5
	$\bar{x}$	2.04	1.91	2.03	2.27
	s	0.22	0.18	0.16	0.094
	C.V.	10.61	9.47	8.01	4.14
	S.E. _m	0.017	0.023	0.024	0.014
n	O.R.	10-14	10-14	11-14	11-14
	$\bar{x}$	12.46	12.37	12.50	12.78
	s	0.38	0.39	0.37	0.48
	C.V.	3.07	3.17	2.97	3.79
	S.E. _m	0.029	0.051	0.054	0.071
n/dt	O.R.	4.76-9.16	5.71-9.16	5.20-8.12	5.00-6.19
	$\bar{x}$	6.16	6.55	6.18	5.63
	s	0.55	0.55	0.41	0.052
	C.V.	8.97	8.37	6.62	0.92
	S.E. _m	0.043	0.071	0.059	0.0077
Graphs:—					
n/dt	r	0.93	0.92	0.72	0.98
	a	1.77	2.17	2.28	5.15
	b	8.86	8.23	7.86	1.09
n/dt / dt	r	-0.96	-0.96	-0.91	-0.46
	a	-2.56	-3.04	-2.52	-0.55
	b	11.38	12.33	11.30	6.89

	A	At	At/A	Graph:—At/A	
O.R.	0.36-0.89	0.026-0.041	0.037-0.081	r	0.32
$\bar{x}$	0.55	0.032	0.063	a	0.027
s	0.21	0.0055	0.017	b	0.018
C.V.	37.69	17.09	26.12		
S.E. _m	0.092	0.0025	0.0061		

other cases, the septal ends are free, or fused in groups of two or three in the centre of the tabularium.

Usually the dissepiments are uniserial between adjacent septa and appear rather closely spaced in cross-section. Around the tabularium, and coincidental with the septal thickening, the traces of a single series of horseshoe dissepiments form two

strong concentric walls (Pl. 3, fig. 1), or delimit the width of the single thick wall when the septa are in lateral contact (Pl. 3, fig. 3).

In longitudinal-section, the dissepimentarium is composed of several rows of small, globose dissepiments, usually between 0.1 and 0.3 mm. in height. Immediately adjacent to the tabularium, the dissepiments are quite sharply modified into a vertical series of horseshoes, predominantly uniserial and quite regularly developed. The surface of the dissepimentarium slopes steeply away from the series of horseshoe dissepiments but is flat over most of its area. The tabularium junction is sharply defined.

Tabularium structure is not perfectly clear from the present material. The tabulae appear to be closely spaced and usually incomplete. Often there is a wide peripheral series of horizontal plates, slightly distally concave, abutting against a central series of small, flat-topped or occasionally globular domes, which occupy a third to a quarter of the tabularium diameter. In other portions of the tabularium, this axial structure is missing and the whole width is occupied by flat, interleaved plates.

Four examples of lateral increase have been seen in BM (NH) R5616 although in each case the new individuals are well advanced.

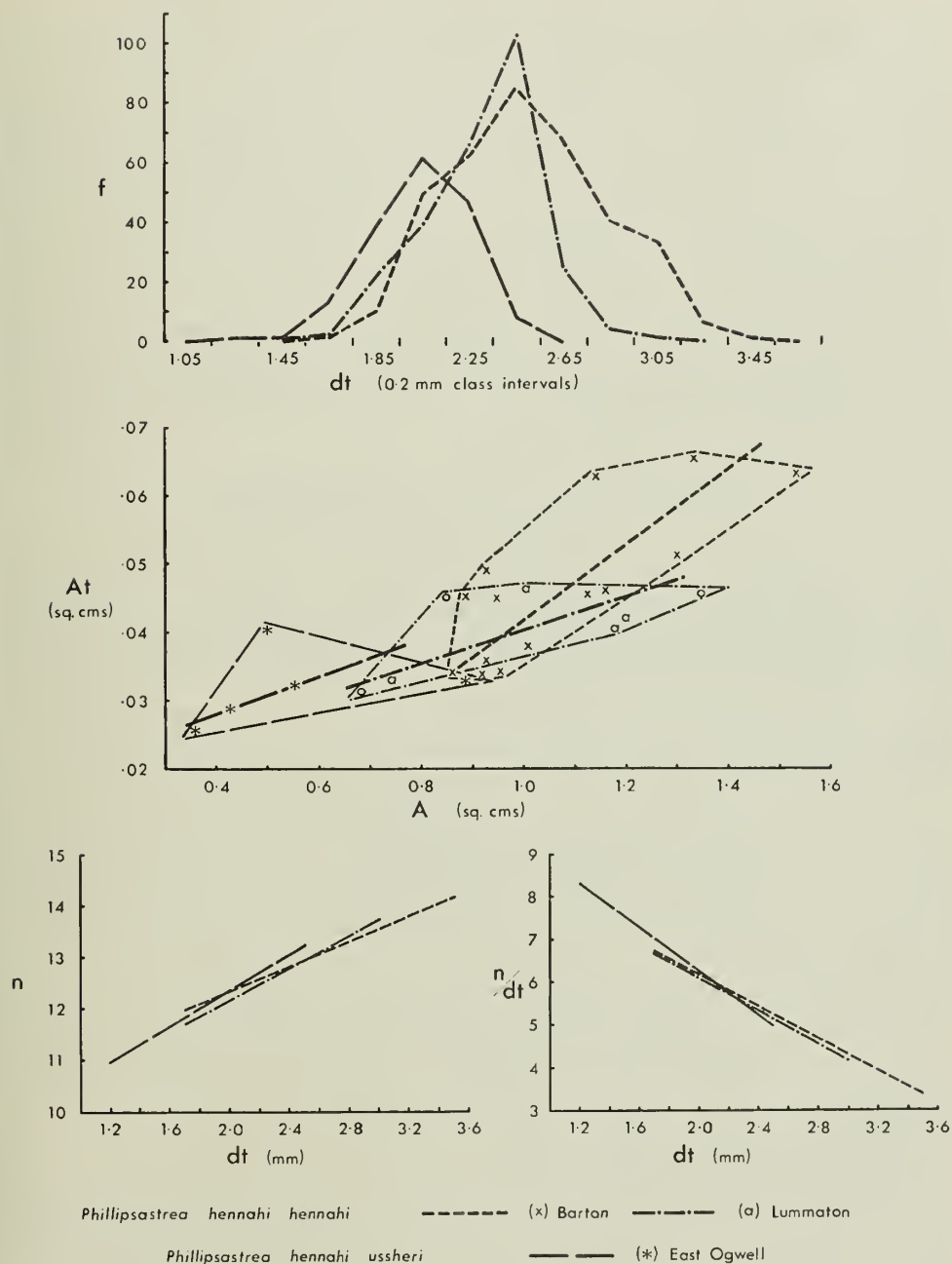
A small sample of five colonies of this subspecies has been statistically analysed. Three of the colonies have also been treated separately to investigate colonial variation. The resulting statistics are given in Table 5 and the data illustrated graphically in Text-figs. 11 and 12.

DISCUSSION. It is possible that some of the material from Upper Devonian localities in continental Europe which has been described as *Phillipsastrea hennahi* properly belongs to this subspecies; for example, the specimen figured by Frech (1885, pl. 5, fig. 2) from the Frasnian Ibergerkalk at Bad Grund, Germany.

Comparison of the subspecies of Phillipsastrea hennahi. The main quantitative characteristics of *P. hennahi hennahi* (Barton Quarry sample) and *P. hennahi ussheri* have been statistically compared and the results are tabulated below:

dt	t = 14.69 (524° freedom)	P << 0.01
n/dt	z (slope) = 7.38	P << 0.01
At/A	z (slope) = 1.91	P > 0.01
	z (position) = 7.02	P << 0.01

The mean tabularium diameter for *P. hennahi ussheri* (2.04 mm.) is significantly smaller than that for *P. hennahi hennahi* (2.45 mm.). There is also a significant difference between the slopes of the correlation lines on the graph plotting *n* against *dt* for the two subspecies. The number of major septa increases slightly faster with increasing tabularium diameter in the Frasnian subspecies. The number of points on the graph plotting *At* against *A* is rather low to allow the results of a "z" test to be uncritically accepted (Imbrie 1956 : 237, footnote 1). Nevertheless, the significant difference in position reflects the small degree of overlap of the points for the two subspecies.



Qualitatively the two subspecies are very similar and obviously closely related. The strong cross-sectional traces of horseshoe dissepiments, usually infilled by close packed septal tissue, which surrounds the tabularium in *P. hennahi ussheri* is, however, very distinctive. The horseshoe traces are rarely so clearly seen in *P. hennahi hennahi* and excessive septal dilatation is similarly uncommon. The major septa within the tabularium are also contrasted in the two subspecies. The abrupt attenuation of the septa, which closely approach the axis, often with a lobate thickening of their axial ends, is characteristic of *P. hennahi ussheri*. The major septa of *P. hennahi hennahi* are usually somewhat withdrawn from the axis and taper away from the dilated zone.

In longitudinal-section, the most noticeable difference between the two subspecies is in the tabularium structure. The narrow axial domes and wide, flat peripheral plates of *P. hennahi ussheri* contrast with the broad based, flat-topped domes of *P. hennahi hennahi*. There is, however, no characteristic difference between the dissepimentaria of the two subspecies.

Phillipsastrea devoniensis (Edwards & Haime)

Plate 4, figs. 1-4

- 1851 *Pachyphyllum devoniense* Edwards & Haime : 397.
 1853 *Pachyphyllum devoniense* Edwards & Haime; Edwards & Haime : 234, pl. 52, figs. 5, 5a.
 1883 *Pachyphyllum devoniense* Edwards & Haime; C. F. Roemer : 393, text-fig. 93.
 1885 *Phillipsastrea (Pachyphyllum) devoniense* (Edwards & Haime) Frech : 67, pl. 6, figs. 2, 2a.
 1952 *Pachyphyllum devoniense* Edwards & Haime; Soshkina : 86.

But not:

- 1958 *Pachyphyllum devoniense* Edwards & Haime; Bulvanker : 93, pl. 45, figs. 1a, b.

DIAGNOSIS. Astraeoid tending to thamnasterioid *Phillipsastrea* with poorly defined corallite margins. Mean tabularium diameter 3.72 mm. with 16 to 23 major septa (South Devon sample). Septa generally thin, with slight, elongate dilatation surrounding tabularium. In longitudinal-section, a series of horseshoe dissepiments is developed just outside tabularium junction. Tabulae wide, flat, complete or incomplete.

HOLOTYPE. The original of Edwards & Haime's (1853, pl. 52) fig. 5 and 5a; Devonian, Torquay. This specimen is either mislaid or lost.

MATERIAL. "Rocky Valley". Measured specimens: OUM D277, BM(NH) 74489.

?Lummaton Quarry. Measured specimen: TM(JB) 105.

Torquay, S. Devon: BM(NH) R1456.

DISTRIBUTION. England: *in situ* only from middle Givetian limestones, Wolborough Quarry, Newton Abbot and ?from upper Givetian limestones, Lummaton Quarry, Torquay. Other specimens are beach pebbles, several being known from "Rocky Valley" (? = Valley of Rocks, Watcombe, north of Torquay). Also recorded from the Ibergerkalk, Bad Grund, Germany; Frasnian.

DESCRIPTION. Nothing is known of the overall size, shape and external features of this species.

Colonies are astraeoid tending to thamnasterioid. The septa are usually outwardly geniculate and irregularly abutting. Occasionally they may be perfectly confluent from one corallite to the next or rarely they end in the dissepimentarium with a free peripheral end. The margins of the corallites are indistinctly defined in the absence of a well formed pseudotheca.

The septa, major and minor, are 0.1 mm. or less in thickness in the dissepimentarium where they follow a straight or sinuous course. In a zone surrounding the tabularium of 1 to 1.5 mm. width, the septa have a slight, elongate dilatation, usually to about 0.2 or 0.3 mm. thickness. Minor septa project just within the tabularium. The major septa continue in a strongly attenuate form more or less to the axis, where their ends may be free and infrequently slightly thickened, or confluent with septa in the adjacent quadrant of the tabularium. Carinae are not developed.

Dissepiments are usually uniserial between adjacent septa. Just outside the tabularium, in the zone of septal dilatation, cross-sectional traces of horseshoe dissepiments are often clearly visible. The tabularium junction is clearly defined.

In longitudinal-section, the dissepimentarium is composed of several series of arched dissepiments usually between 0.2 and 0.4 mm. high. Just outside the tabularium, a slightly discontinuous single series of irregularly sized horseshoe dissepiments is developed. From the crest of the series, the dissepiments slope steeply downwards towards the corallite margins where they become flat lying. On the axial side of the horseshoes, one or two rows of normal dissepiments are usually present.

The tabularium, which is more or less sharply delimited from the dissepimentarium, is composed of wide, flat or gently undulating plates, usually slightly downturned peripherally. The tabulae are complete or incomplete and a periaxial series of sloping plates is intermittently developed.

Insufficient material is available for a statistical study of variation in this species. The few measurements made are summarized in Table 6.

DISCUSSION. The present material agrees very well with Edwards & Haime's (1853 : 234, pl. 52, figs. 5, 5a) figures and descriptions, although their original specimen appears to have had somewhat larger tabularia. Frech's (1885) figures of a specimen from the Ibergerkalk (Harz, Germany) are very close to the illustrations of the holotype and to the present material, although the horseshoe dissepiments in the German specimen appear stronger and more regularly developed.

Phillipsastrea devoniensis differs markedly from *P. hennahi* in both tabularium size and septal number. In addition, the horseshoe dissepiments of the former are somewhat less regular in size and, unlike those of *P. hennahi*, are separated from the tabularium by steep sloping normal dissepiments. The thin elongate septal dilatation in *P. devoniensis* (Pl. 4, fig. 2) also contrasts with the markedly spindle-shaped septa of *P. hennahi* (Pl. 1, fig. 1).

P. devoniensis is similar in many respects to *P. bouchardi* and *P. ibergensis*. Both the latter species, however, have slightly different tabularium structure and *P. bouchardi* has much larger tabularia (dt = 10-16 mm. according to Semenoff-Tian-

Chansky 1961 : 307) than *P. devoniensis*. *P. ibergensis* is further distinguished by strong spindle shaped septal dilatation.

The specimen figured by Bulvanker (1958, pl. 45, figs. 1a, b) as *P. devoniense* has considerably larger tabularia than the English material. It is closer in size to *P. bouchardi* and also has the slightly sagging tabularium structure of that species in contrast to the flat or faintly domed tabulae of *P. devoniensis*.

P. devoniensis is an uncommon species. Very few specimens have been seen in English museums and the author has found none in the field. It appears that Frech's (1885 : 67) specimen is the only record of the species from abroad.

Phillipsastrea ananas (Goldfuss)

Plate 5, figs. 1-4

1826 *Cyathophyllum ananas* Goldfuss : 60 pars, pl. 19, fig. 4b, non 4a.

1851 *Acervularia troscheli* Edwards & Haime : 416.

1885 *Phillipsastrea ananas* (Goldfuss) Frech : 49 pars, pl. 2, figs. 1, 2, 5, 5a, 5b, pl. 3, ?fig. 5; pl. 8, ?fig. 9.

1953 *Pseudoacervularia ananas* (Goldfuss) Rózkowska : 52, text-figs. 27, 28, pl. 7, figs. 1, 2.

But not:

1881 *Heliophyllum troscheli* (Edwards & Haime); Schlüter : 203, pl. 4, figs. 3, 4.

DIAGNOSIS. Pseudocerioid *Phillipsastrea*. Mean tabularium diameter 3.54 mm. with 14-18 major septa (East Oggwell sample). Septa thin peripherally, with slim, spindle-shaped dilatation near tabularium boundary. Major septa usually form weak axial vortex. Dissepimentarium reflexed, with imperfect series of horseshoe dissepiments at crest from which two or three rows of normal dissepiments slope steeply into tabularium. Axial tabulae flat-topped domes with peripheral horizontal concave plates.

TYPE SPECIMEN. The original specimen figured by Goldfuss (1826, pl. 19, fig. 4b) is either mislaid or lost. Frasnian; Namur, Belgium.

MATERIAL. BM (N.H.) R46158-9. Road cutting, south side, 30-35 yd. west of Ramsleigh Quarry entrance, East Oggwell, near Newton Abbot; Lower Frasnian.

DISTRIBUTION. England: Lower Frasnian; East Oggwell, near Newton Abbot. Also widespread in Frasnian of Namur, Belgium; Harz, Stolberg near Aachen, Germany; Kielce region, Poland; Urals, Kuznetsk Basin, U.S.S.R.

DESCRIPTION. The material consists of fragments of apparently pseudocerioid coralla. The epitheca is predominantly straight but may be zigzagged.

The septa, both major and minor, are spindle-shaped. At the periphery they are about 0.05 mm. across but the major septa may dilate up to 0.45 mm. thick near the tabularium junction. The maximum length of septal thickening is about 2 mm. The septa may be carinate. BM (N.H.) R46159 (Pl. 5, fig. 3) has well developed yardarm carinae, up to 0.25 mm. across with a minimum spacing of 0.15 mm., on many but not all septa. BM (N.H.) R46158 (Pl. 5, fig. 2) on the other hand has only rarely developed, very faint, carinae.

The minor septa do not penetrate the tabularium but the major septa continue, much attenuated, almost to the axis where they usually form a weak vortex. There is usually an axial area 0.2–0.4 mm. in diameter which is free of septa.

The dissepiments may be uni- or multiserial between septa. The tabularium junction is not strongly marked but coincides approximately with the axial ends of the minor septa.

TABLE 6.—Quantitative comparison of some species and subspecies of *Phillipsastrea*.

	dt		n	n/dt	At/A
	O.R.	$\bar{x}$	O.R.	$\bar{x}$	$\bar{x}$
<i>P. hennahi hennahi</i>	1.7–3.5	2.45	10–16	5.25	0.045
<i>P. hennahi ussheri</i>	1.2–2.5	2.04	10–14	6.16	0.063
<i>P. devoniensis</i>	3.0–5.0	3.72	16–23	5.04	ca. 0.1
<i>P. ananas</i>	3.0–4.0	3.54	14–18	4.44	ca. 0.15
<i>P. rozkowskæ</i>	2.3–2.9	2.64	12–15	5.08	ca. 0.1

In longitudinal-section, the dissepimentarium is of variable width, and the dissepimental surface strongly reflexed with the crest on average 0.6 mm. outside the tabularium. The dissepiments at the crest are usually modified to horseshoe shape, forming a slightly discontinuous vertical series of horseshoe dissepiments. There are several rows of normal dissepiments towards the margins of the corallites and on the other side of the crest, two or three rows of dissepiments slope steeply into the tabularium.

The tabulae are complete or incomplete flat-topped domes, occupying about three-fifths of the tabularium diameter. There is a peripheral series of horizontal, distally concave plates.

The two known specimens from East Ogvell have slightly different quantitative data which is averaged in Table 6. Individually, BM (N.H.) R46159 has tabularium diameters of 3 to 3.5 mm. with 14 or 15 major septa whilst BM (N.H.) R46158 has 3.8 to 4.0 mm. tabularium diameters with 15 to 18 major septa.

DISCUSSION. Although the two specimens described here differ slightly in some respects, they both appear to fall within the range of variation shown by *P. ananas* in areas where the species is more abundant. On the other hand, they also show some features which are intermediate in character with *P. macrommata* (F. A. Roemer).

Frech (1885 : 49) considered these two species to be synonymous whilst Rózkowska (1953 : 49–52) was able to distinguish between them in Poland through the lower septal-tabularium ratio, the short, strong septal dilatation and the slightly different dissepimental arrangement in *P. macrommata*. The English material agrees in general morphological appearance with *P. ananas* of Rózkowska. On the other hand, the septal insertion in both the present specimens follows more closely the curve for *P. macrommata* given by Rózkowska (1957, text-fig. 26).

In view of the limited material, the two specimens are placed in *P. ananas* on morphological grounds. They may, however, need re-evaluation if a larger sample ever becomes available from East Ogvell.

Phillipsastrea rozkowskae sp. nov.

Plate 6, figs. 1-4

DERIVATION OF NAME. The species is named after Professor Maria Rózkowska (Poznań, Poland).

DIAGNOSIS. Pseudocerioid *Phillipsastrea*. Tabularium diameter 2.3-2.9 mm. with 12 to 15 major septa (topotype sample). Septa of two orders, major with short, club-shaped dilatation against tabularium boundary, becoming extremely attenuate in tabularium; minor septa hardly thickened. Dissepiments in several rows with single vertically discontinuous series of horseshoe dissepiments. Tabularium structure simple, with incomplete tabulae.

HOLOTYPE. BM(NH) R46156. Lower Frasnian; road cutting, south side, 25 yd. west of Ramsleigh Quarry entrance, East Ogwell, near Newton Abbot.

MATERIAL. BM(NH) R46156-57. Horizon and locality as for holotype.

DISTRIBUTION. Type locality only.

DESCRIPTION. Massive, pseudocerioid colonies with predominantly pentagonal corallites separated by straight to slightly zigzagged pseudothecae. Only two fragments are available and details of colony shape, size and external features are unknown.

The septa, major and minor, are 0.05-0.15 mm. thick peripherally. They are generally straight but may occasionally be very slightly flexed in the dissepimentarium. The major septa are dilated up to 0.35 mm. across for a length of 0.6 to 1 mm. just outside the tabularium. The minor septa are only slightly thickened in the same area. The latter do not penetrate the tabularium but the major septa, extremely attenuated, extend usually to within 0.4 mm. of the axis where they are usually curved into a very faint vortex. There is no dilatation of the axial ends of the major septa. Carinae are not developed and the septa are usually smooth throughout.

Dissepiments are usually uniserial between adjacent septa. The trace of the horseshoe dissepiments, corresponding in position with the septal dilatation, forms a well marked wall around the tabularium.

In longitudinal-section, the dissepimentarium is composed of several series of variably shaped dissepiments, from near flat to quite globose. Just outside the tabularium, the dissepimental surface rises to a crest formed by a somewhat discontinuous vertical series of horseshoe dissepiments. Steep sloping vesicles are occasionally developed between the horseshoe dissepiments and the tabularium.

The structure of the tabularium is simple. Tabulae are incomplete, distally concave plates or low elongate vesicles. They are arranged to give a flat or slightly concave surface to the tabularium.

The few data available for the species are summarized in Table 6.

DISCUSSION. *P. rozkowskae* is probably the species of *Phillipsastrea* which most closely approaches *Frechastraea*. Its septa are very similar to the typical

frechastreaid form (see p. 232) and the series of horseshoe dissepiments is relatively poorly developed for *Phillipsastrea*.

P. rozkowskae is similar in its pseudocerioid growth form to *P. smithi* (Rózkowska), *P. ananas* (Goldfuss) and *P. macrommata* (F. A. Roemer). It differs from the latter two, however, through its smaller tabularium size and lower *At/A* ratio as well as the character of its septal thickening. *P. smithi* is distinguished by very strong septal dilatation forming a wide, dense wall around the tabularium. On the axial side of this wall, the major septa are represented by thick lobes only, and do not cross the tabularium towards the axis.

Genus *FRECHASTRAEA* nov.

DERIVATION OF NAME. The genus is named after Fritz Frech (1861-1917).

DIAGNOSIS. Massive rugose corals, pseudocerioid, astreaeoid or thamnasterioid. Corallites small with clearly defined wall at tabularium junction. Septa of two orders, major and minor, generally slightly thickened against tabularium junction and strongly attenuate in tabularium. In longitudinal-section, dissepiments small, globose. Septal trabeculae arranged in a fan usually on the series of dissepiments adjacent to tabularium. Horseshoe dissepiments may rarely occur in this series. Dissepimental surface almost flat with a slight elevation surrounding tabularium. Tabulae complete or incomplete.

TYPE SPECIES. *Cyathophyllum pentagonum* Goldfuss (1826 : 60, pl. 19, fig. 3). Frasnian; Namur, Belgium.

DISTRIBUTION. Widespread in the Frasnian of Europe.

Other species assigned to *Frechastrea*. *Acervularia goldfussi* de Verneuil & Haime (1850 : 161); ?*Smithia boloniensis* Edwards & Haime (1851 : 423); *Smithia bowerbanki* Edwards & Haime (1851 : 423); *Smithia micrommata* C. F. Roemer (1852 : 197, pl. 5¹, figs. 20a, b); ?*Acervularia roemeri* var. *β concinna* F. A. Roemer (1855 : 32, pl. 6, figs. 19a-c); *Phillipsastrea sanctacrucensis* Rózkowska (1953 : 59, text-figs. 32-33, pl. 2, figs. 8-10); *Phillipsastrea pentagona* (Goldfuss) var. *minima* Rózkowska (1953 : 66, text-figs. 36-38, pl. 8, fig. 9).

DISCUSSION. *Frechastrea* embraces a well defined group of Devonian colonial rugose corals. Species here included in the genus have been previously assigned to *Hexagonaria*, *Billingsastrea*, *Phillipsastrea* or synonyms of these three genera.

Workers in the last century, particularly Edwards & Haime, frequently placed pseudocerioid and astreaeoid Devonian corals, including species of *Frechastrea*, in the Silurian genus *Acervularia* Schweigger. This similarity between the Silurian and Devonian forms is, however, quite superficial and *Acervularia* has long been considered unrelated to the phillipsastreids. More or less concurrent with the use of *Acervularia*, some astreaeoid and thamnasterioid species of *Frechastrea* were assigned to *Smithia*, which is an objective synonym of *Phillipsastrea*.

Lang & Smith (1935 : 559) referred to *Prismatophyllum pentagona* (Goldfuss) in their remarks on the genus *Prismatophyllum*. *Prismatophyllum* Simpson is con-

sidered a junior synonym of *Hexagonaria* Gürich (see Lang, Smith & Thomas 1940 : 104). The type species of both, *P. prisma* Lang & Smith and *H. hexagona* (Goldfuss) respectively, are characterized by typical disphyllid dissepimentaria with the septal trabeculae sloping axially and upwards throughout. *Frecheastraea* differs from these chiefly by the possession of a full trabecular fan based on the series of dissepiments adjacent to the tabularium. In addition, *Hexagonaria* shows no tendency to the development of horseshoe dissepiments and lacks the strongly defined tabularium junction characteristic of the present genus.

Many of the forms assigned to *Hexagonaria* by Moenke (1954) also do not possess a disphyllid dissepimentarium. These species, however, are morphologically quite distinct from those referred to *Frecheastraea* and have been placed in *Marisastrum* by Rózkowska (1965 : 262) and Scrutton (1967 : 270).

Schouppé (1958 : 235) included species of *Frecheastraea* in the genus *Billingsastraea* Grabau. The type species of *Billingsastraea* is *B. verneuli* (Edwards & Haime). The holotype is missing but Ehlers & Stumm (1953 : 2) have described corals under that name which appear in all respects to satisfy the original diagnosis. *Billingsastraea sensu stricto* is thus characterized by a broadly reflexed dissepimentarium in which there is no tendency to produce horseshoe dissepiments. The septa are uniformly thin from the periphery to the axis of the corallite, usually with no sign of dilatation, and the strongly marked tabularium junction of *Frecheastraea* is lacking. Oliver (1964 : 2-3) criticized Schouppé's interpretation of *Billingsastraea* and suggested that there is probably no close relationship between that genus and the phillipsastraeids. The writer subscribes to this view (Scrutton 1967 : 276) and species of *Frecheastraea* are here considered quite distinct from *Billingsastraea*.

Schouppé (1958 : 156) recorded a well developed series of horseshoe dissepiments in *P. hennahi*, the type species of *Phillipsastrea*. Until that time, species of *Frecheastraea* had been widely assigned to that genus. They are certainly most closely related to *Phillipsastrea* but may be distinguished from it by the rarity with which horseshoe dissepiments occur. *Frecheastraea* is also strongly characterized by its septa (compare Text-figs. 4b & 4c)—uniformly thick in the dissepimentarium with a short club-shaped thickening against the tabularium boundary, and major septa strongly attenuate in the tabularium. In *Phillipsastrea* the septa are more spindle-shaped, and may be equally thin in the tabularium and peripheral parts of the dissepimentarium; frecheastraeid type septa are only rarely known. Finally species of *Frecheastraea* tend to have smaller individuals—seldom greater than 2mm. tabularium diameter—than species of *Phillipsastrea*.

The occasional horseshoe dissepiments developed in the dissepimentaria of species of *Frecheastraea* are recorded here for the first time. It is thought that the genus descended from a phillipsastreid ancestor chiefly through the progressive elimination of horseshoes from the dissepimentarium. *P. rozkowskiae*, in particular, shows a tendency toward frecheastraeid characters and is considered a possible intermediary between the two genera. It may be significant in an evolutionary sense that Rózkowska (1953) did not record horseshoes in species of *Frecheastraea* from mainly Upper Frasnian horizons in Poland whilst they can often be seen in the dissepimentaria of the same species among the English Lower Frasnian material.

Frechastraea pentagona pentagona (Goldfuss)

Plate 6, fig. 5; Plate 7, figs. 1-5

- 1826 *Cyathophyllum pentagonum* Goldfuss : 60, pl. 19, fig. 3.
 1840 *Astrea (Favastrea) pentagona* (Goldfuss) Lonsdale : 697 *pars*, pl. 58, fig. 1 (*non 1a*).
 1841 *Astrea pentagona* (Goldfuss); Phillips : 11, pl. 6, fig. 15.
 1851 *Acervularia pentagona* (Goldfuss) Edwards & Haime : 418.
 1853 *Acervularia pentagona* (Goldfuss); Edwards & Haime : 238, pl. 53, figs. 5-5b.
 1883 *Acervularia pentagona* (Goldfuss); C. F. Roemer : 352, text-fig. 70.
 1885 *Phillipsastrea pentagona* (Goldfuss) Frech : 54 *pars*, pl. 3, figs. 7, 7a, 7b, 10; pl. 8, fig. 3.
 1935 *Prismatophyllum pentagona* (Goldfuss) Lang & Smith : 559.
 1953 *Phillipsastrea pentagona* (Goldfuss); Rózkowska : 64, text-figs. 36-39, pl. 8, fig. 7.

But not:

- 1952 *Phillipsastrea pentagona* (Goldfuss); Soshkina : 102, pl. 43, fig. 145.

DIAGNOSIS. Pseudocerioid *Frechastraea* with mean tabularium diameter 1.09 mm. and 7 to 13 major septa (East Oggwell sample). Smooth, non-carinate septa. Horseshoe dissepiments very rarely developed. Tabulae complete or incomplete. Increase axial or lateral.

LECTOTYPE (selected by J. W. Pickett *in press*). Original of Goldfuss 1826, pl. 19, fig. 3 which is specimen 206 in the Goldfuss Collection of the Geologisch-Paläontologisches Institut, Bonn. Goldfuss (1826 : 60) gave the horizon and locality as the "Transition limestone of the Namur region", Belgium. Frasnian.

MATERIAL. Ramsleigh Quarry: OUM D279 (Colony 1), BM(NH) R23400 (Colony 3), BM(NH) R5635 (Colony 4). Other measured specimens: BM(NH) R676, TM(JB) 305A.

Road cutting, 20 yd. west of Ramsleigh Quarry entrance: OUM D538 (Colony 2). Other measured specimen: OUM D537.

Road cutting, 40 yd. west of Ramsleigh Quarry entrance. Measured specimen: OUM D532.

DISTRIBUTION. England: Lower Frasnian limestones, Ramsleigh Quarry and adjacent road cutting, East Oggwell, near Newton Abbot, south Devon. Also Frasnian of Belgium, Germany and Poland.

DESCRIPTION. Colony shape, external features and overall dimensions are unknown as all the English material is fragmentary. Rózkowska (1953 : 64), however, described Polish representatives of this subspecies as thick, tabular colonies up to 6 cm. in diameter and 6 cm. in height. Goldfuss' original specimen is a thick, rectangular block with the convex upper surface measuring 7 cm. by 8 cm. The corallites have slightly depressed tabularia with a low, encircling ridge formed by the innermost series of dissepiments. Rózkowska gave no details of a holotheca and it is not preserved in any of the English specimens.

The colonies are massive, pseudocerioid, tending rarely to astraeoid or thamnasterioid. Individual corallites, usually pentagonal or hexagonal in shape, are separated from each other by a straight or zigzagged pseudotheca. Occasionally the pseudotheca may break down when the septa are more or less confluent from one corallite to the next.

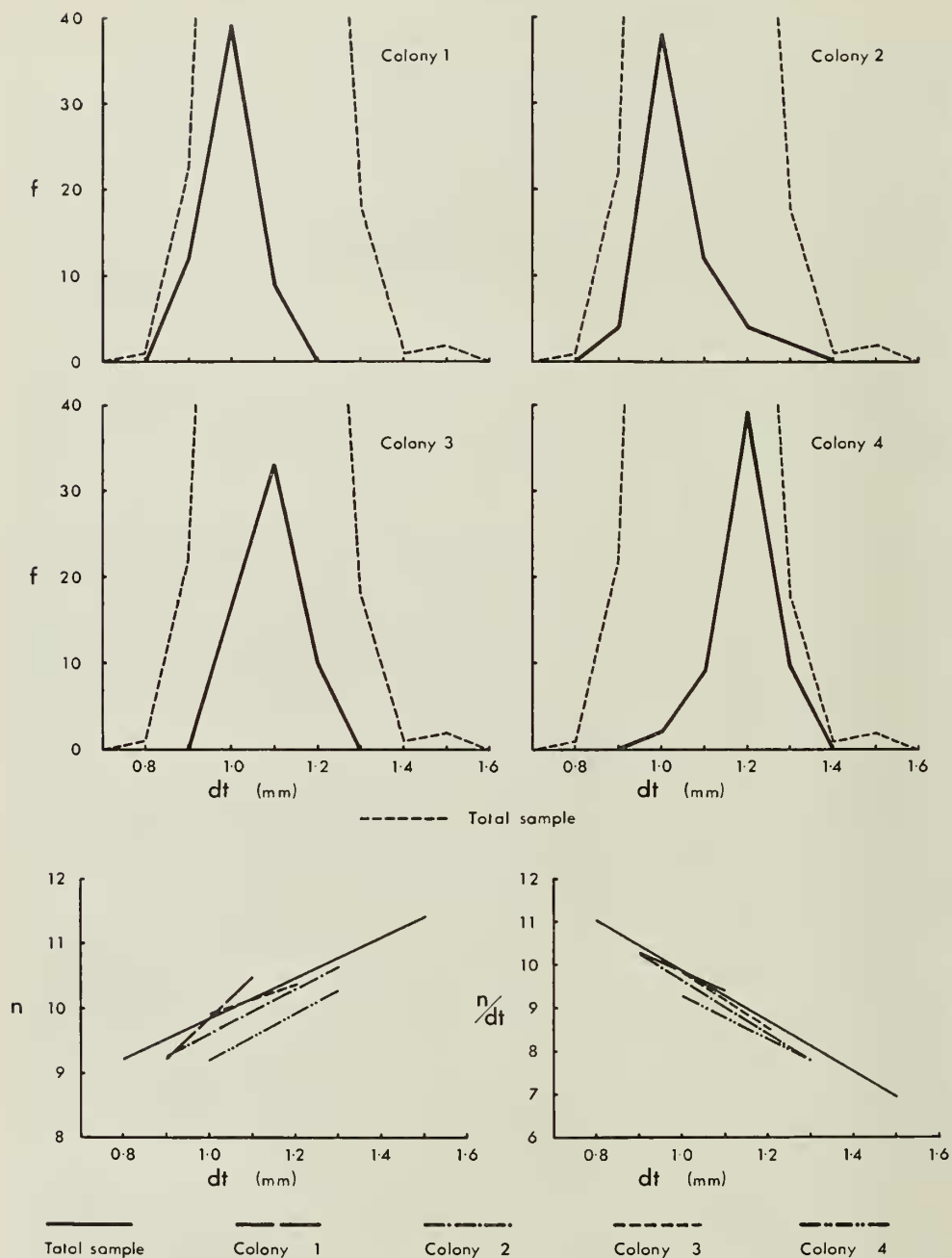
FIG. 13. *Frechastraea pentagona pentagona*.

TABLE 7.—Statistical data for some characters of *Frecheastraea pentagona pentagona*.

		Total sample N	Colony 1 60	Colony 2 60	Colony 3 60	Colony 4 60
dt	O.R.	0.8-1.5	0.9-1.1	0.9-1.3	1.0-1.2	1.0-1.3
	$\bar{x}$	1.09	1.00	1.04	1.09	1.20
	s	0.10	0.059	0.084	0.067	0.068
	C.V.	9.38	5.97	8.13	6.12	5.65
	S.E. _m	0.005	0.0077	0.011	0.0086	0.0087
n	O.R.	7-12	7-11	8-11	9-12	9-12
	$\bar{x}$	10.12	9.80	9.73	10.12	9.90
	s	0.32	0.38	0.30	0.15	0.24
	C.V.	3.15	3.85	3.04	1.48	2.43
	S.E. _m	0.016	0.049	0.038	0.019	0.031
n/dt	O.R.	6.67-12.00	7.78-11.11	7.69-10.00	8.33-10.00	7.50-10.00
	$\bar{x}$	9.36	9.86	9.73	9.32	8.30
	s	0.59	0.25	0.30	0.44	0.33
	C.V.	6.34	2.54	3.04	4.69	3.93
	S.E. _m	0.029	0.032	0.038	0.056	0.042
Graphs:—						
n/dt	r	0.92	0.94	0.74	0.99	0.91
	a	3.13	6.35	3.51	2.25	3.57
	b	6.72	3.49	6.09	7.67	5.63
n/dt/ td	r	-1.00	-0.90	-0.96	-0.99	-0.94
	a	-5.81	-4.21	-6.10	-6.56	-4.83
	b	15.68	14.05	15.75	16.42	14.07

	A	At	At/A	Graph:—At/A	
O.R.	0.091-0.16	0.0078-0.011	0.057-0.099		
$\bar{x}$	0.12	0.0093	0.079	r	0.38
s	0.024	0.0013	0.015	a	0.055
C.V.	20.25	14.38	18.63	b	0.0027
S.E. _m	0.0086	0.00047	0.0052		

The septa, both major and minor, are straight and uniformly thick, about 0.05 mm. across, in the dissepimentarium. At the tabularium junction the major septa, and to a lesser degree the minor, are dilated to form a short bulbous thickening. This thickening, associated with the clearly defined junction between tabulae and dissepiments, gives rise to a strong internal wall at this point. The minor septa are normally confined to the dissepimentarium and only occasionally show as slight projections into the tabularium. The major septa, however, continue into the tabularium as extremely thin processes, usually extending halfway or slightly more towards the axis and sometimes reaching the axis itself. There is a strong tendency for the axial ends of the longer major septa to fuse. The thin septal elements in the tabularium

are easily obliterated by slight recrystallization, but even in the best of the material examined there was no sign of thickening of the axial ends of the major septa.

The dissepiments are almost always uniserial between adjacent septa and appear moderately spaced in cross-section. In longitudinal-section, the dissepimentarium is composed of several series of small, evenly developed, well arched dissepiments. Their vertical height varies between 0.1 and 0.2 mm. The dissepimental surface is usually flat but may occasionally slope slightly away from the tabularium boundary. At the latter position, a dissepiment may very rarely be modified into a horseshoe shape but there is no tendency to develop a series of horseshoe dissepiments. No more than two, or possibly three horseshoes have been observed in continuous vertical succession.

The tabularium structure is often partially obscured by slight recrystallization. The tabulae are usually flat lying and may be complete or interleaved. Occasionally, however, they slope downwards away from the axis with an overall tent or bell shaped appearance. In some cases there is evidence of axial structures suggesting the vesicles described in the tabularium of *Frechastraea goldfussi* (see p. 249). Unfortunately, poor preservation and sometimes septal traces obscure the axial area at these points and the relationships of the tabulae are not clear. In the more simply constructed tabularia, the tabulae have an average vertical spacing of about 0.2 mm.

Both axial and lateral increase have been observed in this subspecies, the latter being more common.

A sample of eight colonies from the limestones exposed in Ramsleigh Quarry and the adjacent road cutting has been statistically analysed. Four of the colonies have also been analysed individually. The statistics are listed in Table 7 and illustrated graphically in Text-figs. 13 and 16.

DISCUSSION. Both Lonsdale (1840 : 697) and Frech (1885 : 54) included *Acer-vularia goldfussi* or specimens belonging to this species in their interpretation of *Cyathophyllum pentagonum*. The two species are superficially extremely similar, although on close inspection they can be readily distinguished. The details of the differences are given below (p. 253) under *F. goldfussi*.

The most recent thorough investigation of *Frechastraea pentagona pentagona* is by Rózkowska (1953 : 64) as a species of *Phillipsastrea*. Her material has a slightly larger mean tabularium diameter than the English sample but there is no doubt that they belong to the same subspecies.

Frechastraea pentagona (Goldfuss) *minima* (Rózkowska)

Plate 8, figs. 1-3

1953 *Phillipsastrea pentagona* (Goldfuss) var. *minima* Rózkowska : 66, text-figs. 36-38, pl. 8, fig. 9.

1953 *Phillipsastrea bowerbanki* (Edwards & Haime); Rózkowska : 67, pl. 8, figs. 3, 4.

1959 *Phillipsastrea pentagona* (Goldfuss) var. *micrommata* (C. F. Roemer); Middleton : 156, text-fig. 6f.

DIAGNOSIS. Pseudoceroid to astraeoid to thamnasterioid *Frechastraea*. Mean tabularium diameter 0.96 mm. with 7 to 12 major septa (East Oggwell sample).

Tabularia somewhat unevenly spaced. Septa sinuous and only slightly dilated at tabularium junction. Horseshoe dissepiments rare. Increase axial or lateral.

HOLOTYPE. Ag8 in the Collections of the Polska Akademia Nauk, Pracownia Palaeozoologii, Poznań, Poland. Upper Frasnian, Psie Górki, Kielce, Poland.

MATERIAL. Ramsleigh Quarry: GSM 73119 (Colony 1), GSM 11822 (Colony 2), GSM 73118 (Colony 3). Other measured specimens: BM(NH) R46371, BM(NH) R23266. Additional material: GSM 11821, GSM 11823.

DISTRIBUTION. England: Lower Frasnian of Ramsleigh Quarry, East Oggwell, near Newton Abbot, south Devon. Also Upper Frasnian of Kielce, Poland.

DESCRIPTION. Details of size, shape and external features of the English material are unknown as it is fragmentary. Rózkowska (1953 : 67), however, described the holotype as a low, plate-like colony measuring 3.5 cm. by 1.6 cm. in surface area.

Individual corallites are seldom completely surrounded by an external pseudotheca and usually the septa are confluent or subconfluent between them. All gradations from the pseudocerioid to the thamnasterioid stage are usually present in the same colony and this is accompanied by a general increase in the distances separating the tabularia. Where an external pseudotheca is present, it is formed by the deflection of the peripheral septal ends.

The septa, 0.05 mm. or less in thickness, are uniformly thin and are gently sinuous between tabularia. They are usually smooth sided. Rarely there appears to be a slight separation of the trabeculae, which remain unthickened, resulting in discontinuous septa. At the tabularium junction, the septa are slightly dilated for about 0.1 mm. of their length. Within the tabularium, the major septa thin abruptly and continue as very fine filaments more or less to the axis, where the ends of two or more adjacent septa may fuse. The minor septa do not penetrate into the tabularium.

The dissepiments are almost always uniserial between adjacent septa. The tabularium junction is sharply defined in cross-section, giving the appearance of an internal wall.

In longitudinal-section, the dissepimentarium is composed of several series of small, well arched dissepiments. They may vary somewhat in size and their height, usually about 0.1 mm., ranges from 0.05 to 0.25 mm. The surface of the dissepimentarium is flat peripherally, usually rising slightly with the more globose dissepiments adjacent to the tabularium. Horseshoe dissepiments may rarely develop in the latter position.

The tabularium structure is simple and the tabulae may be complete or incomplete. The complete tabulae are either flat or sag slightly in the middle. The incomplete tabulae are flat to slightly bowed and interleaved with each other, or in the form of long weakly arched vesicles. The vertical spacing of the tabulae may vary between 0.1 and 0.3 mm., but is normally about 0.15 mm. in the more regularly developed tabularia.

Examples of both axial and lateral increase have been observed.

A statistical analysis has been made of a total sample of 5 colonies from Ramsleigh

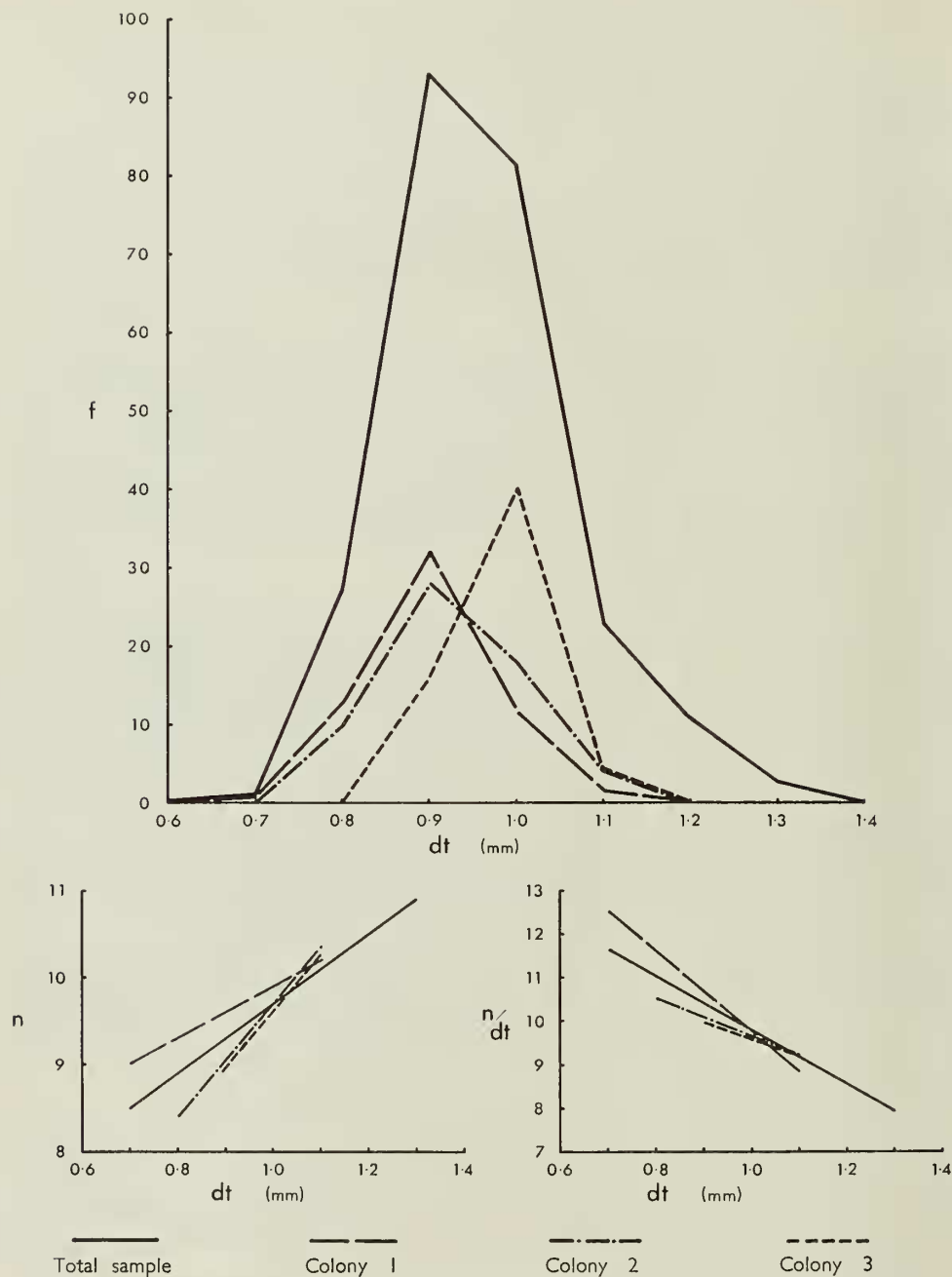
FIG. 14. *Frechastraea pentagona minima*.

TABLE 8.—Statistical data for some characters of *Frecheastraea pentagona minima*.

	N	Total sample 240 (5)	Colony 1 60	Colony 2 60	Colony 3 60
dt	O.R.	0.7-1.3	0.7-1.1	0.8-1.1	0.9-1.1
	$\bar{x}$	0.96	0.90	0.93	0.98
	s	0.11	0.079	0.082	0.055
	C.V.	10.98	8.78	8.85	5.57
	S.E. _m	0.0068	0.010	0.011	0.0071
n	O.R.	7-12	8-10	7-11	8-10
	$\bar{x}$	9.54	9.61	9.25	9.52
	s	0.42	0.23	0.54	0.36
	C.V.	4.42	2.42	5.86	3.77
	S.E. _m	0.027	0.030	0.070	0.046
n/dt	O.R.	7.69-12.87	8.18-12.87	7.78-11.26	8.89-11.12
	$\bar{x}$	10.05	10.72	10.01	9.72
	s	0.64	0.73	0.35	0.20
	C.V.	6.40	6.82	3.54	2.04
	S.E. _m	0.42	0.094	0.046	0.026

Graphs:—

n/dt	r	0.98	0.77	0.95	0.97
	a	4.00	2.94	6.61	6.58
	b	5.71	6.96	3.12	3.07
n/dt/ dt	r	-0.98	-0.99	-0.88	-0.92
	a	-6.11	-9.24	-4.32	-3.63
	b	15.91	19.06	14.01	13.27

	A	At	At/A	Graph:—At/A	
O.R.	0.11-0.15	0.0065-0.010	0.054-0.071	r	0.84
$\bar{x}$	0.12	0.0075	0.062	a	0.092
s	0.017	0.0016	0.0076	b	-0.0036
C.V.	14.52	21.37	12.21		
S.E. _m	0.0078	0.00072	0.0034		

Quarry. Three of these colonies have also been analysed individually. The statistics are listed in Table 8 and illustrated graphically in Text-figs. 14 and 16.

DISCUSSION. Różkowska (1953 : 66) erected this subspecies as a variety of "*Phillipsastraea pentagona*" on only one specimen. Although the tabularia of her specimen (0.6-0.8 mm. diameter) are slightly smaller than those in the English examples, the colonies are in complete morphological agreement and are undoubtedly the same subspecies. The holotype clearly shows the characteristic pseudocerioid grading to thamnasterioid nature of the corallites and the irregular spacing of the tabularia described above.

The specimen described by Rózkowska (1953 : 67) as "*Phillipsastraea bowerbanki*" is indistinguishable from GSM 73118 (Pl. 8, fig. 1) of the present material and is thus also referable to this subspecies. The slight morphological differences between these specimens and the holotype of *F. pentagona minima* lie within the range of variation to be expected. *F. pentagona minima* is quite distinct from *F. bowerbanki* which is almost exclusively thamnasterioid and has considerably larger tabularia, wide and regularly spaced (see p. 253).

Two fragments from Ramsleigh Quarry (GVM 26/7 and 26/8), misidentified as *Phillipsastraea pentagona* var. *micrommata* by Middleton (1959 : 156), also belong to this subspecies.

F. pentagona pentagona and *F. pentagona minima* are very similar in quantitative terms. Only 0.13 mm. separates their mean tabularium diameters. In addition, their lines on the graphs plotting septal number against tabularium diameter and tabularium area against corallite area are very similar in both slope and position (Text-fig. 16). Nevertheless, because of the large sample sizes, tests of statistical discrimination show the subspecies to differ significantly in both *dt* (Table 10) and their lines on the former of the two graphs.

F. pentagona minima is distinguished principally on qualitative characteristics, and without prior separation on these grounds, could not be differentiated from *F. pentagona pentagona* on quantitative data alone. *F. pentagona pentagona* is pseudoceroid, tending slightly to astraeoid, with straight septa. The septa in *F. pentagona minima*, on the other hand, are generally sinuous and associated with a wide range in form from pseudoceroid to thamnasterioid. The tabularia also tend to be irregularly spaced. In the material so far examined, no difficulty has been found in distinguishing quite clearly between the two subspecies.

Both occur in association in the Lower Frasnian Ramsleigh limestones in England and the Upper Frasnian of Kielce in Poland (Rózkowska 1953). In the English fauna, *F. pentagona pentagona* and *F. pentagona minima* occur in approximately equal numbers whilst Rózkowska's figures suggest a ratio of 11 : 1 in favour of *F. pentagona pentagona* in the Kielce area.

Frechastraea micrommata (C. F. Roemer)

Plate 8, figs. 4, 5

1852 *Smithia micromata* C. F. Roemer : 197, pl. 5¹, figs. 20a, b.

But not:

1885 *Phillipsastrea pentagona* (Goldfuss) var. *micrommata* (C. F. Roemer) Frech : 56, pl. 3, figs 11-13; pl. 8, fig. 1.

1953 *Phillipsastraea pentagona* (Goldfuss) var. *micrommata* (C. F. Roemer); Rózkowska : 66, text-figs. 36-38; pl. 8, fig. 8.

1958 *Phillipsastraea pentagona* (Goldfuss) var. *micrommata* (C. F. Roemer); Bulvanker : 123, pl. 60, figs. 1-3; pl. 61, figs. 4, 5.

1959 *Phillipsastraea pentagona* (Goldfuss) var. *micrommata* (C. F. Roemer); Middleton : 156, text-fig. 6f.

DIAGNOSIS. Pseudoceroid tending to astraeoid *Frechastraea*. Mean tabularium diameter 1.42 mm. with 18 to 21 septa (holotype). Major and minor septa not

distinguished as septa penetrating the tabularium exceedingly rare; septa non-carinate. Tabularium structure very simple, usually composed of complete tabulae. Increase lateral.

LECTOTYPE (here chosen). Specimen no. 34 in the collections of the Geologisch-Paläontologisches Institut, Bonn. Original of Roemer's (1852, pl. 5¹) figures 20a, b. Frasnian; Ferques near Boulogne, France.

DESCRIPTION. Colony irregularly disc shaped, 8 cm. in diameter and 4 cm. high; covered basally by a strongly concentrically ridged holotheca. The corallites are pseudoceroid tending to astraeoid with a thin, usually zigzagged, pseudotheca.

The septa are not normally distinguished as major and minor as with very rare exceptions they all end at the tabularium junction. The septa are about 0.05 mm. thick in the dissepimentarium and follow a straight or slightly sinuous course to the tabularium boundary where they may thicken slightly. Septa may occasionally form slight inward projections on the tabularium boundary and one septum was seen to penetrate the tabularium for a distance of 0.4 mm.

The tabularium-dissepimentarium junction is a thin strong circular wall in cross-section. This wall appears to be the product of septal dilatation and thickening of the inner arms of the series of dissepiments adjacent to the tabularium. Sometimes, however, the septa themselves appear to bend sharply at the boundary to form a segment of the wall.

In longitudinal-section, the dissepimentarium is composed of several series of quite globose dissepiments normally 0.5–0.6 mm. in height. In narrow levels which can be traced from corallite to corallite, however, they become smaller, flatter and more closely spaced. The dissepimental surface is flat over most of its area but rises slightly to a crest adjacent to the tabularium. Horseshoe dissepiments have not been observed.

Tabularium structure is very simple, consisting in the main of complete flat or slightly bowed tabulae with occasional incomplete arched plates. The latter may be subsidiary to the complete tabulae or may interleaf to form the tabularium structure proper.

One example of lateral increase has been observed.

Measurements on twelve corallites showed tabularium diameter to range from 1.3–1.5 mm., mean value 1.42 mm., with 18 to 21 septa. Mean n/dt , taking n to be half the number of septa in each corallite, is 6.94.

DISCUSSION. The above description is based on Roemer's figured specimen only. Although no horseshoe dissepiments have been observed, the character of the species as a whole places it without doubt in *Frechastrea*. Full knowledge of the variation in dissepimental shape must await the description of further material belonging to this species.

This is the first time that the type specimen has been sectioned and the slides show that Frech (1885 : 56) and subsequent authors have misidentified the species. The specimens placed by Frech and others in *Smithia micrommata* (as *Phillipsastrea pentagona* var. *micrommata*) are here assigned to *F. carinata* sp. nov. which is described below.

F. micrommata differs from all other known species of *Frechastraea* by the lack of any distinction between major and minor septa. In particular, it can be distinguished from *F. carinata* by the latter's septal carination and more complex tabularium structure. Data so far available show that tabularia in *F. micrommata* are somewhat larger than in *F. carinata* ($\text{dt}\bar{x} = 1.02 \text{ mm.}$).

Frechastrea carinata sp. nov.

Plate 9, figs. 1-3

1885 *Phillipsastrea pentagona* (Goldfuss) var. *micrommata* (C. F. Roemer) Frech : 56, pl. 3, figs. 11-12, ?13; pl. 8, ?fig. 1.

1953 *Phillipsastrea pentagona* (Goldfuss) var. *micrommata* (C. F. Roemer); Rózkowska : 66, text-figs. 36-38, pl. 8, fig. 8.

But not:

1852 *Smithia micrommata* C. F. Roemer : 197, pl. 5¹, figs. 20a, b.

1958 *Phillipsastrea pentagona* (Goldfuss) var. *micrommata* (C. F. Roemer); Bulvanker : 123, pl. 60, figs. 1-3; pl. 61, figs. 4-5.

1959 *Phillipsastrea pentagona* (Goldfuss) var. *micrommata* (C. F. Roemer); Middleton : 156, text-fig. 6f.

DERIVATION OF NAME. The name refers to the presence of septal carinae, an important distinguishing feature of this species.

DIAGNOSIS. Pseudocerioid, tending to astraeoid and thamnasterioid *Frechastraea*. Mean tabularium diameter 1.02 mm. and between 8 and 14 major septa (topotype sample). Septa variably but typically carinate. Horseshoe dissepiments very rare. Tabulae mainly incomplete. Increase axial or lateral.

HOLOTYPE. OUM D309. Lower Frasnian; road cutting, 80 yd. west of Ramsleigh Quarry entrance, East Ogwell, near Newton Abbot, south Devon.

MATERIAL. Ramsleigh Quarry: BM(NH) R23210 (Colony 1), BM(NH) R23211 (Colony 2), BM(NH) R23216 (Colony 3), BM(NH) R5640 (Colony 4). Other measured specimens: BM(NH) R677, BM(NH) R5634.

Road cutting, 80 yd. west of Ramsleigh Quarry entrance. Measured material: OUM D309-310, OUM D535-6.

DISTRIBUTION. England: Lower Frasnian limestones, Ramsleigh Quarry and the adjacent road cutting, East Ogwell, near Newton Abbot, south Devon. Also Frasnian of Germany (Harz) and Poland (Kielce).

DESCRIPTION. Nothing is known of colony shape, size and external features from the present material.

The colonies are pseudocerioid, tending to astraeoid and occasionally thamnasterioid in parts. Corallites are irregularly polygonal, usually pentagonal or hexagonal, and for the most part separated from each other by a straight or slightly zigzagged wall formed by the deflection of the peripheral septal ends. When this pseudotheca breaks down, the geniculate ends of the septa are more or less confluent with those of the adjacent corallite.

The septa, of two orders major and minor, are variable in thickness but average about 0.05 mm. in the dissepimentarium where they may be sinuous. Occasionally

corallites have a bilateral appearance when the septa tend to lie parallel on either side of the tabularium. Within the tabularium, the major septa thin considerably to about 0.02 mm. in thickness and continue, as straight or flexuous filaments, more or less to the axis. Minor septa are confined to the dissepimentarium. Sometimes the axial ends of adjacent major septa fuse, or the axial ends of opposite septa are continuous across the tabularium. Signs of thickening of the axial ends of septa are very rare.

The septa are variably carinate in the dissepimentarium. In exceptional cases the carinae may reach 0.4 mm. in width, but mostly they are between 0.1 and 0.15 mm. Their spacing varies but normally there are 10 carinae per mm. of septal length. On individual septa, carination is heaviest in a zone of irregular width surrounding the tabularium, corresponding to the septal dilatation observed in *Frechastraea pentagona* and *F. goldfussi*; occasionally, adjacent carinae may fuse along the septa in this zone. As they enter the tabularium, the septa rapidly become smooth.

The dissepiments, moderately to closely spaced in cross-section, are almost exclusively uniserial between adjacent septa. The tabularium junction is sharply defined.

In longitudinal-section the dissepimentarium consists of several series of regularly developed, small, arched dissepiments. Their height is usually between 0.1 and 0.2 mm. The dissepiments become progressively more globose towards the tabularium and against the tabularium boundary, horseshoe dissepiments occur very rarely. The surface of the dissepimentarium slopes slightly downwards and outwards from the tabularium and is flat lying peripherally.

The tabularium structure is usually simple. The tabulae are commonly incomplete and may be flat or moderately arched. Their vertical spacing averages about 0.2 mm. In one specimen, OUM D310b, there is evidence of highly domed axial plates, occupying about one fifth of the tabularium diameter, with peripheral flat, or slightly bowed tabulae. This axial structure is not clearly developed but it appears to be similar to that described in *F. goldfussi*.

Very few instances of increase have been observed but both axial and lateral are represented.

A total sample of ten colonies from Ramsleigh Quarry and the adjacent road cutting has been statistically analysed. Four of the colonies have also received individual treatment. The statistics are listed in Table 9 and illustrated graphically in Text-figs. 15, 16.

DISCUSSION. Material assigned to this new species was formerly known, due to Frech's (1885 : 56) work, as '*Phillipsastrea pentagona* var. *micrommata* (C. F. Roemer)'. Recently, however, the writer has been able to section Roemer's figured specimen of *Smithia micrommata*, which is described above. This shows conclusively that Frech and all subsequent workers have wrongly interpreted Roemer's species.

Frech also placed *Acervularia roemeri* var. *β concinna* F. A. Roemer in synonymy with his *P. pentagona* var. *micrommata*. The original material of the former variety appears to be missing and F. A. Roemer's illustrations (1855, pl. 6, figs. 19a-c) are

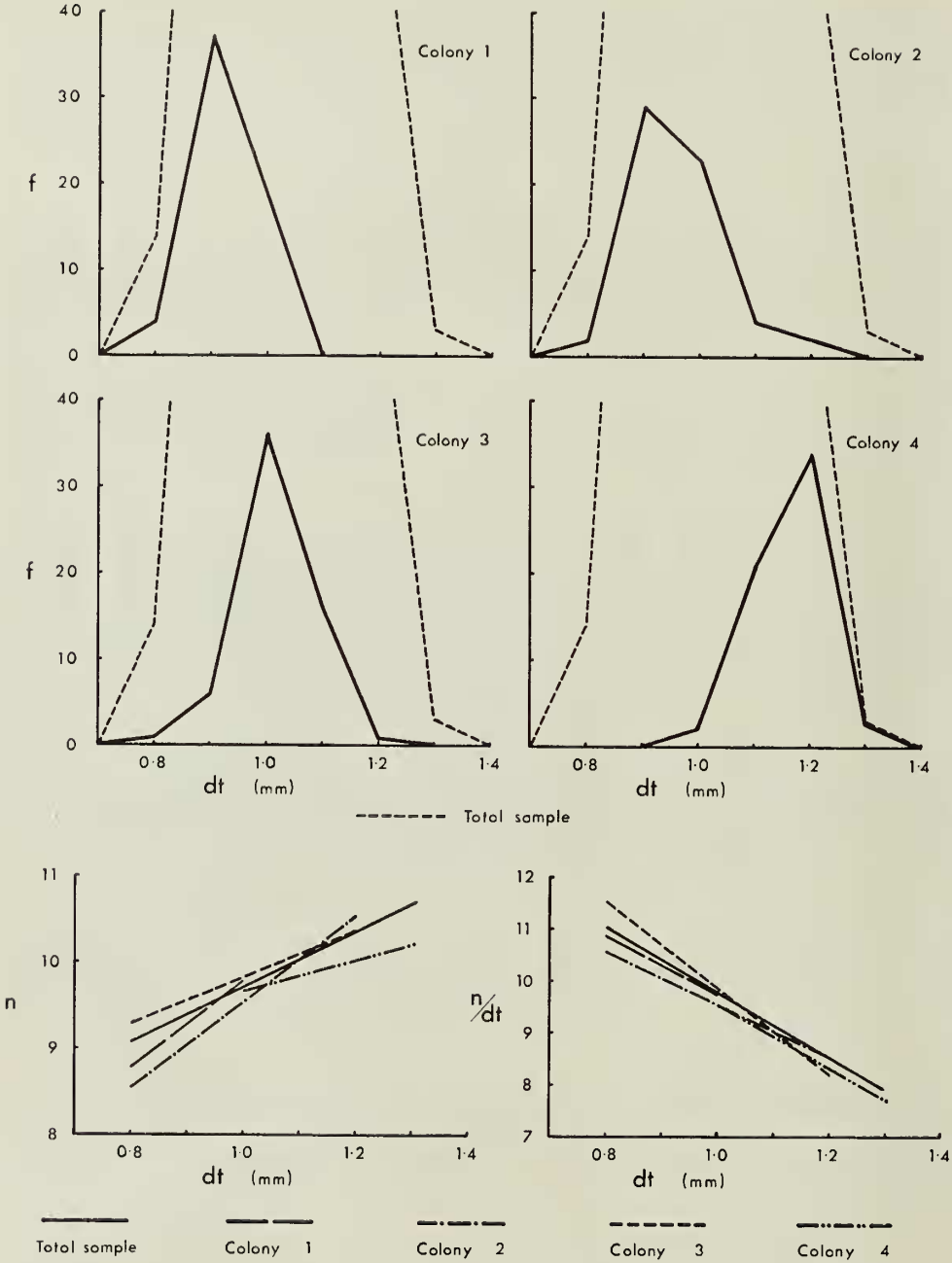


FIG. 15. *Frechastraea carinata*.

rather poor. They show no sign of septal carinae, however, and the septa themselves are spindle-shaped and thin peripherally—the phillipsastreid rather than the frechastraeid pattern. The present material is thus considered distinct from *A. roemeri* var. *β concinna*.

F. carinata is extremely close quantitatively to *F. pentagona*, with its mean tabularium diameter falling between that of *F. pentagona pentagona* and *F. pentagona minima* (Text-fig. 16). Statistical discrimination however reflects the high sample

TABLE 9.—Statistical data for some characters of *Frechastraea carinata*.

		Total sample	Colony 1	Colony 2	Colony 3	Colony 4
	N	423 (9)	60	60	60	60
dt	O.R.	0.8–1.3	0.8–1.0	0.8–1.2	0.8–1.2	1.0–1.3
	$\bar{x}$	1.02	0.93	0.96	1.02	1.16
	s	0.11	0.057	0.081	0.069	0.064
	C.V.	10.56	6.18	8.44	6.81	5.47
	S.E. _m	0.0052	0.0074	0.010	0.0090	0.0082
n	O.R	8–14	8–10	8–11	8–11	9–11
	$\bar{x}$	9.75	9.42	9.35	9.87	9.95
	s	0.34	0.29	0.40	0.19	0.12
	C.V.	3.51	3.07	4.29	1.89	1.18
	S.E. _m	0.017	0.037	0.052	0.024	0.015
n/dt	O.R.	7.27–12.73	8.89–11.26	8.00–11.11	8.33–12.50	7.50–12.50
	$\bar{x}$	9.66	10.20	9.79	9.74	8.57
	s	0.68	0.32	0.41	0.58	0.39
	C.V.	7.07	3.13	4.22	5.90	4.50
	S.E. _m	0.033	0.041	0.053	0.074	0.050
Graphs:—						
n/dt	r	0.95	1.00	0.93	0.70	0.89
	a	3.18	5.07	4.96	2.69	1.84
	b	6.52	4.73	4.60	7.13	7.82
n/dt / dt	r	—1.00	—1.00	—0.96	—0.96	—1.00
	a	—6.36	—5.59	—5.11	—8.30	—6.06
	b	16.12	15.37	14.69	18.18	15.62

	A	At	At/A	Graph:—At/A	
O.R.	0.10–0.17	0.0067–0.011	0.052–0.088		
$\bar{x}$	0.13	0.0082	0.063	r	0.77
s	0.024	0.0013	0.011	a	0.054
C.V.	18.45	15.86	17.68	b	0.0012
S.E. _m	0.0081	0.00044	0.0037		

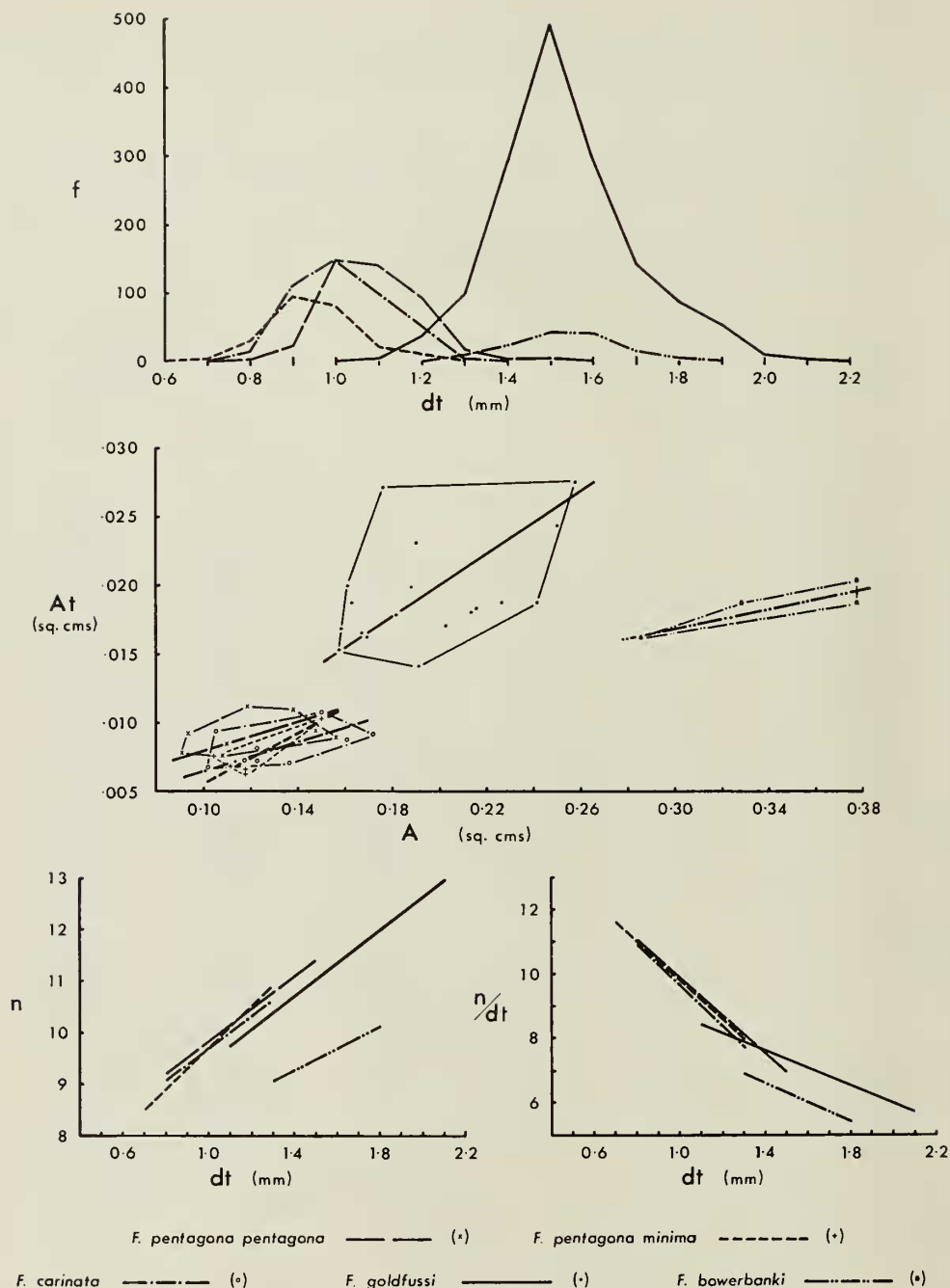


FIG. 16. Graphical comparison of some quantitative characters for the species and sub-species of *Frechastraea*.

TABLE 10.—Statistical discrimination between some characters for species and subspecies of *Frechastraea*. Significant values in bold; s = slope, p = position.

		<i>pentagona</i> <i>pentagona</i>	<i>pentagona</i> <i>minima</i>	<i>carinata</i>	<i>goldfussi</i>	<i>bowerbanki</i>
Values of "t":—						
dt	<i>pentagona pentagona</i>		15.388	9.838	55.924	
	<i>pentagona minima</i>	15.388		6.589		
	<i>carinata</i>	9.838	6.589			
	<i>goldfussi</i>	55.924				0.149
	<i>bowerbanki</i>				0.149	
Values of "z":—						
n/dt	<i>pentagona pentagona</i>	s		11.041	0.724	
		p		6.946		
	<i>pentagona minima</i>	s	11.041	11.335		
		p				
	<i>carinata</i>	s	0.724	11.335	1.562	
		p	6.946		10.426	
	<i>goldfussi</i>	s		1.562		13.855
		p		10.426		
	<i>bowerbanki</i>	s			13.855	
		p				
At/A	<i>pentagona pentagona</i>	s		1.326	0.379	2.196
		p		0.116	4.533	3.724
	<i>pentagona minima</i>	s	1.326		1.544	0.719
		p	0.116		0.000	3.496
	<i>carinata</i>	s	0.379	1.544		
		p	4.533	0.000		
	<i>goldfussi</i>	s	2.196	0.719		3.719
		p	3.724	3.496		
	<i>bowerbanki</i>	s				
		p			3.719	

sizes and *F. carinata* can be shown to be significantly different from both subspecies in **dt** and the plot of **n** against **dt**, and from *F. pentagona pentagona* alone in the plot of **At** against **A** (Table 10).

Qualitatively, *F. carinata* is distinguished by its sinuous, variably carinate septa. There is also a characteristic tendency for the majority of the septa in one corallite to follow the same directional trend in the dissepimentarium. *F. sanctacrucensis* (Rózkowska), recorded so far only from Poland, is closest in general appearance to *F. carinata*. The former is clearly astraeoid, however, with considerably larger tabularia (**dt** ca. 2 mm., **n** 12–14), and its septal carination gives a distinctive "string-of-pearls" effect.

Frechastraea goldfussi (de Verneuil & Haime)

Plate 10, figs. 1–5; Plate 11, figs. 1, 2

1826 *Cyathophyllum ananas* Goldfuss : 60 *pars*, pl. 19, fig. 4a (*non* fig. 4b).

1840 *Astrea* (*Favastrea*) *pentagona* (Goldfuss) Lonsdale : 697 *pars*, pl. 58, fig. 1a (*non* fig. 1).

1850 *Acervularia goldfussi* de Verneuil & Haime : 161.

- 1851 *Acervularia goldfussi* de Verneuil & Haime; Edwards & Haime : 417.
 1851 *Acervularia limitata* Edwards & Haime : 419.
 1853 *Acervularia goldfussi* de Verneuil & Haime; Edwards & Haime : 236, pl. 53, figs. 3, 3a.
 1853 *Acervularia limitata* Edwards & Haime; Edwards & Haime : 238, pl. 54, ?figs. 1, 1a.
 1881 *Acervularia pentagona* (Goldfuss); Schlüter : 89, pl. 9, figs. 4, 5.
 1883 *Acervularia goldfussi* de Verneuil & Haime; C. F. Roemer : 352.
 1883 *Acervularia limitata* Edwards & Haime; C. F. Roemer : 353.
 1885 *Phillipsastrea ananas* (Goldfuss) Frech : 49 *pars*.
 1885 *Phillipsastrea pentagona* (Goldfuss) Frech : 54, *pars*, pl. 3, ?figs. 6, 9.
 1951 *Phillipsastraea limitata* (Edwards & Haime); Soshkina : 97, pl. 17, fig. 2; pl. 18, fig. 2; pl. 23, fig. 4.
 1952 *Phillipsastraea limitata* (Edwards & Haime); Soshkina : 101, pl. 42, fig. 142.
 1953 *Phillipsastraea goldfussi* (Edwards & Haime); Rózkowska : 62, text-figs. 35-37, pl. 8, figs. 5, 6.
 1958 *Billingsastraea goldfussi* (Edwards & Haime) Schouppé : 236, text-figs. 25, 26.
 1959 *Phillipsastraea goldfussi* (Edwards & Haime); Middleton : 156, text-fig. 6d.

But not:

- 1881 *Heliophyllum* cf. *limitatum* (Edwards & Haime) Schlüter : 87, pl. 8, figs. 1, 2.

DIAGNOSIS. Pseudocerioid *Frechastraea*. Mean tabularium diameter 1.53 mm. and between 7 and 17 major septa (East Ogwell sample). Septa smooth, very rarely carinate, usually with lobate thickening on axial ends of major septa. Dissepimentarium occasionally with imperfect series of horseshoe dissepiments at tabularium boundary. Tabularium composed of complete or incomplete tabulae, rarely with axial domes of horseshoe section. Increase axial or lateral.

HOLOTYPE. (see de Verneuil & Haime, 1850 : 161). The original of Goldfuss' (1826, pl. 19, fig. 4a) illustration of *Cyathophyllum ananas*. Frasnian; Namur, Belgium. This specimen is either mislaid or lost.

MATERIAL. Ramsleigh Quarry: TM(JB)310 (Colony 1), BM(NH) R46370 (Colony 2), TM(JB)306 (Colony 3), BM(NH) R23208 (Colony 4), BM(NH) R46369 (Colony 5), TM(JB)307 (Colony 6), BM(NH) R23217 (Colony 7), BM(NH) R46367 (Colony 8), BM(NH) R46368 (Colony 9), BM(NH) R23302 (Colony 10). Other measured specimens: TM(JB)305B, TM(JB)311-313, TM(JB)318, BM(NH) R46374, BM(NH) R5636, BM(NH) R5642, BM(NH) R5648, BM(NH) R23301, OUM D530-1, OUM D539-41.

South Devon: GSM (Geol. Soc. Coll.) 6183.

DISTRIBUTION. England: Lower Frasnian limestones, Ramsleigh quarry, near Newton Abbot, south Devon. Also Frasnian of Belgium, Germany, Poland and U.S.S.R. (Timan); ? Frasnian of Spain.

DESCRIPTION. The specimens are incomplete colonies frequently comprising more than 200 corallites. Colony shape, size and external features are unknown from the present material but according to Rózkowska (1953 : 62) Polish representatives of the species are hemispherical or lenticular colonies up to 7.5 cm. diameter and 3.5 cm. in height, covered basally by a holotheca. Where seen in the English material, the holotheca is about 0.1 mm. thick (Pl. 10, fig. 3). The calices, after Rózkowska, are deep with a flat floor, surrounded by an annular rim at the tabularium boundary.

The colonies are massive, pseudoceroid. The corallites, usually pentagonal or hexagonal, are separated from each other by a strong, straight or more frequently zigzagged pseudotheca. Infrequently the pseudotheca may break down in part when the septa are more or less confluent from one corallite to the next.

In the dissepimentarium the septa, major and minor, are usually about 0.05 mm. but may occasionally reach 0.2 mm. in thickness. They are straight and are variably dilated for a short length against the tabularium boundary. The major septa continue as extremely thin processes across the tabularium to the axis where they develop a variable lobate thickening. Usually these septa are fractionally withdrawn from the axis when their dilated ends form a pseudoaulos. The minor septa, normally less dilated than the major, are not continued beyond the thickened portion which may or may not project slightly into the tabularium. The septa are usually smooth sided but may occasionally be lightly carinate.

The dissepiments appear fairly widely spaced in cross-section and are almost always uniserial between adjacent septa. Occasionally the traces of horseshoe dissepiments can be distinguished around the periphery of the tabularium, corresponding to the zone of septal dilatation. The tabularium junction itself is sharply defined.

In longitudinal-section the dissepimentarium is composed of several series of small, well arched dissepiments. The number of series is variable, however, and may rarely be as low as two. Usually the dissepiments are regularly developed with a height of about 0.2 mm. and become somewhat more globose at the boundary with the tabularium. Occasionally, however, the series immediately adjacent to the tabularium may become modified in part to form an incomplete and irregular series of horseshoe dissepiments. The dissepimental surface slopes away from the tabularium for a short distance and is flat lying peripherally.

The tabularium structure is usually simple, varying from complete flat to slightly domed tabulae, to wide slightly arched incomplete vesicular tabulae. The vertical spacing of the plates varies between 0.1 mm. and 0.5 mm. but is usually about 0.2 mm. Occasionally steep sided complete tabulae with narrow flat crests are developed and rarely highly globose vesicles with a horseshoe-shaped section appear in the axis of the tabularium. When two or three of the latter vesicles are superposed, peripheral plates slope steeply downwards and outwards from them.

Increase is axial or lateral, the latter occurring more commonly.

A statistical analysis has been made of specimens of this species from Ramsleigh Quarry. The total sample comprises 25 colonies, 10 of which have been analysed individually. The statistics are given in Table 11 and the data is presented graphically in Text-figs. 16-18.

DISCUSSION. This species was erected by de Verneuil & Haime (1850 : 1861) in a fossil list, but as they stated that their new species was *Cyathophyllum ananas* Goldfuss (1826, pl. 19, fig. 4a, *non* fig. 4b) their designation is valid. *Acervularia goldfussi* was later described in some detail by Edwards & Haime (1851, 1853) and many subsequent workers have mistakenly attributed the species to these authors.

The lectotype of *Acervularia limitata* Edwards & Haime selected by Soshkina (1951 : 97) is lost and the figure of the specimen (Edwards & Haime 1853, pl. 54,

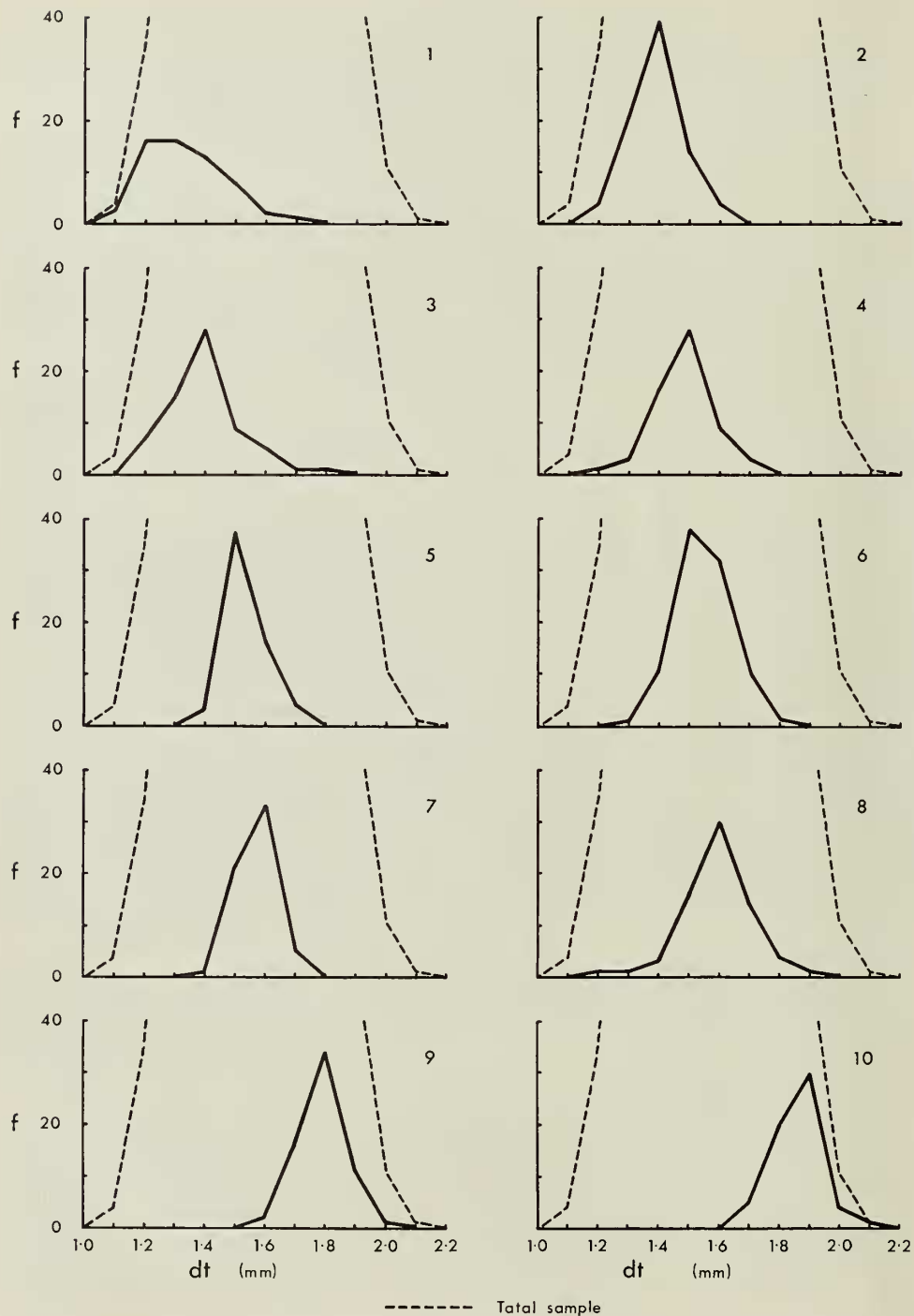
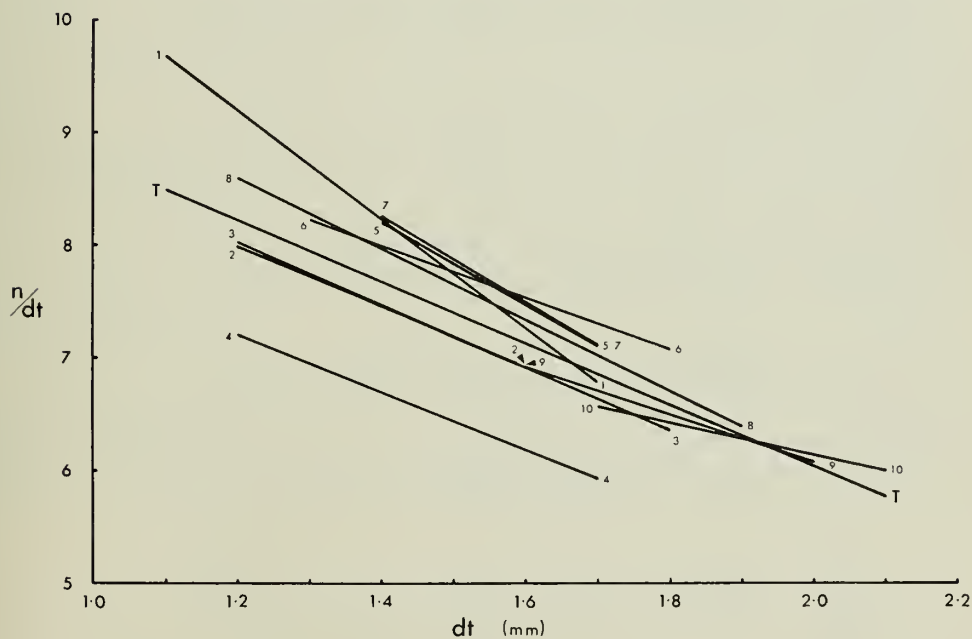
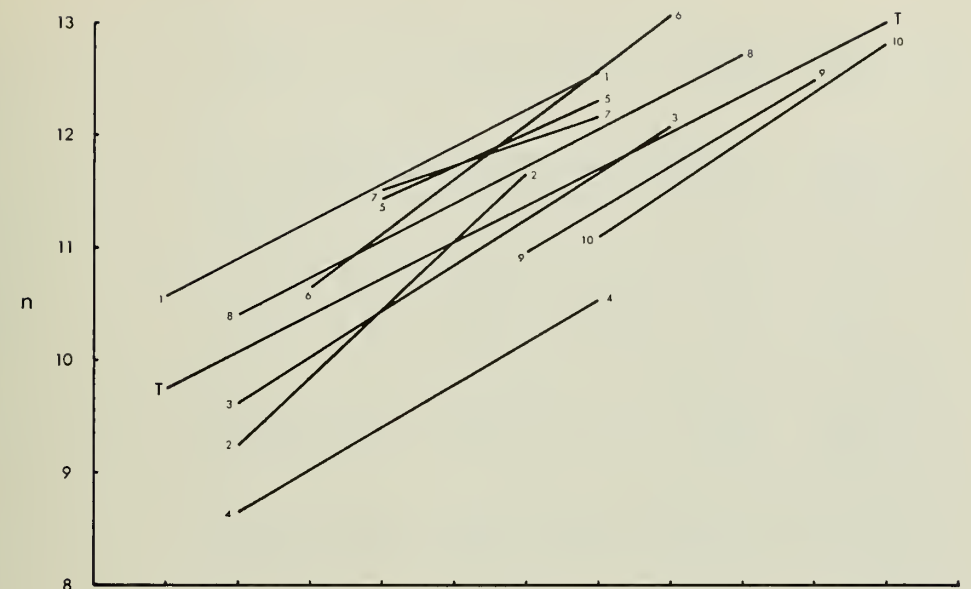


FIG. 17. Tabularium diameter frequency curves for ten colonies of *Frechastraea goldfussi*.



T Total sample

FIG. 18. Graphs of septal insertion and septal-tabularium ratio: tabularium diameter for ten colonies of *Frechastraea goldfussi*.

TABLE 11.—Statistical data for some characters of *Frechastreaa goldfussi*.

	N	Total sample 1,500 (25)	Colony										Colony 9 64	Colony 8 70	Colony 7 60	Colony 6 93	Graph:—At/A
			1	2	3	4	5	6	7	8	9	10					
dt	O.R.	1.1-2.1	1.1-1.7	1.2-1.6	1.2-1.8	1.2-1.7	1.4-1.7	1.3-1.8	1.4-1.7	1.2-1.9	1.6-2.0	1.7-2.1	r	a	b	c	d
	$\bar{x}$	1.53	1.33	1.39	1.40	1.48	1.54	1.55	1.57	1.59	1.79	1.86					
	s	0.16	0.13	0.091	0.12	0.098	0.069	0.092	0.065	0.12	0.078	0.081					
	C.V.	10.10	10.01	6.51	8.75	6.59	4.46	5.92	4.12	7.22	4.35	4.34					
n	S.E.m	0.0040	0.017	0.010	0.015	0.013	0.0088	0.0095	0.0083	0.014	0.0097	0.010	r	a	b	c	d
	O.R.	7-17	9-13	9-13	9-12	8-11	10-13	10-14	11-12	9-12	10-13	10-13					
	$\bar{x}$	11.16	11.32	10.40	10.41	9.60	11.82	11.83	11.90	11.70	11.67	11.77					
	s	0.51	0.44	0.55	0.50	0.35	0.20	0.44	0.14	0.38	0.30	0.35					
n/dt	C.V.	4.57	3.89	5.25	4.78	3.60	1.70	3.74	1.19	3.24	2.55	2.93	r	a	b	c	d
	S.E.m	0.013	0.057	0.060	0.061	0.045	0.026	0.046	0.018	0.045	0.037	0.045					
	O.R.	5.30-9.42	6.47-10.83	6.67-8.57	6.11-9.16	5.29-7.86	6.47-8.57	6.25-8.67	6.88-8.00	6.42-9.17	5.79-7.50	5.72-7.06					
	$\bar{x}$	7.32	8.58	7.49	7.49	6.49	7.71	7.67	7.59	7.36	6.53	6.33					
Graphs:—	s	0.42	0.64	0.24	0.34	0.25	0.25	0.21	0.25	0.36	0.17	0.12	r	a	b	c	d
	C.V.	5.80	7.51	3.22	4.57	3.85	3.27	2.75	3.24	4.92	2.53	1.83					
	S.E.m	0.011	0.084	0.027	0.042	0.032	0.033	0.022	0.032	0.043	0.021	0.015					
	O.R.	0.95	0.63	0.89	0.92	0.90	0.72	0.92	0.78	0.86	0.87	0.94					
n/dt / dt	a	3.27	3.31	6.03	4.07	3.54	2.93	4.83	2.20	3.30	3.83	4.28	r	a	b	c	d
	b	6.14	6.93	2.02	4.73	4.35	7.32	4.36	8.45	6.45	4.83	3.82					
	r	-0.97	-0.93	-0.63	-0.92	-0.86	-0.93	-0.87	-0.98	-0.94	-0.85	-0.86					
	a	-2.72	-4.84	-2.66	-2.80	-2.56	-3.68	-2.31	-3.81	-3.15	-2.12	-1.44					
n/dt / dt	b	11.49	15.01	11.19	11.40	10.28	13.36	11.23	13.57	12.38	10.32	9.00	r	a	b	c	d
	c																
	d																
	e																

figs. 1, 1a) is of uncertain affinity. The only survivor of the original syntypes of *Acervularia limitata* appears to be the specimen figured by Lonsdale (1840 pl. 58, fig. 1a, non fig. 1) as *Astrea* (*Favastrea*) *pentagona* which is GSM (Geol. Soc. Coll.) 6183. This specimen is conspecific with *Frechastraea goldfussi*.

Frech (1885 : 49, footnote) considered *Acervularia goldfussi* as interpreted by Edwards & Haime (1851, 1853) to be transitional in form between his *Phillipsastrea ananas* and '*P.*' *pentagona* and accordingly split the former species between the latter two. This explains the apparent inconsistencies in Frech's synonymies. Under *P. ananas* (p. 49) he placed *Cyathophyllum ananas* Goldfuss (1826 pl. 19, figs. 4a, b) whilst under *P. pentagona* he listed '*Acervularia goldfussi* de Verneuil & Haime 1850 p. 161 *e.p.*'. Frech considered Edwards & Haime's (1853, pl. 53, figs. 3, 3a) figured specimen of *Acervularia goldfussi* as conspecific with his *P. pentagona*.

Most subsequent authors appear to have interpreted *F. goldfussi* on Edwards & Haime's figures and descriptions and to have considered it worthy of specific rank, although closely related to *F. pentagona*. In the absence of Goldfuss' type specimen, this interpretation is followed here. The similarity between *F. goldfussi* and *F. pentagona pentagona* is considerable, both being pseudocerioid with essentially straight, non-carinate septa. Differences are confined to small details such as the lobate thickenings on the axial ends of the major septa in *F. goldfussi* and the higher incidence of horseshoe dissepiments in this species. *F. goldfussi* and *F. pentagona pentagona* are, however, clearly differentiated on quantitative characters (Text-fig. 16 and Table 10). The former has a considerably larger tabularium diameter than the latter and the two are significantly different in their growth lines on graphs plotting *n* against *dt* and *At* against *A*. Both differ strongly from *Phillipsastrea ananas* (described on p. 228) through the larger dimensions, the spindle-shaped septa, complex tabularium and row of well developed horseshoe dissepiments of the latter.

Różkowska (1953 : 62 *et seq.*) has described '*Phillipsastraea*' *goldfussi* in detail from the Upper Frasnian of Poland. Her material has a greater range (1.2–2.8 mm.) and a higher mean value (1.8 mm.) for the tabularium diameter than the English representatives. There is no doubt that the two samples are conspecific, however, and the slight size difference may be due to the higher stratigraphical level of the Polish collection.

Attention is drawn for the first time to the rare horseshoe dissepiments developed in representatives of this species. Besides the English examples, Schlüter (1881, pl. 9, fig. 5) illustrated a specimen as *A. pentagona* referable to this species from the Frasnian of Stolberg, near Aachen (Germany) which also clearly shows occasional horseshoes developed against the tabularium junction.

Frechastraea bowerbanki (Edwards & Haime)

Plate 11, Fig. 3; Plate 12, Figs. 1–3

1851 *Smithia bowerbanki* Edwards & Haime : 423.

1852 *Acervularia seriaca* Quenstedt : 664, pl. 60, fig. 3.

1853 *Smithia bowerbanki* Edwards & Haime; Edwards & Haime : 241, pl. 55, figs. 2, 2a.

1879 *Acervularia seriaca* Quenstedt; Quenstedt : 536, pl. 163, fig. 1.

- 1883 *Phillipsastraea bowerbanki* (Edwards & Haime) C. F. Roemer : 391.
1885 *Phillipsastraea bowerbanki* (Edwards & Haime); Frech : 63, pl. 4, figs. 9, 9a, b.
?1951 *Pachyphyllum bowerbanki* (Edwards & Haime) Soshkina : 89, pl. 16, figs. 1, 2.

But not:

- 1879 *Smithia bowerbanki* Edwards & Haime; Quenstedt : 536, pl. 162, fig. 39.
1953 *Phillipsastraea bowerbanki* (Edwards & Haime); Rózkowska : 67, pl. 8, figs. 3, 4.

DIAGNOSIS. Thamnasterioid *Frechastraea*. Mean tabularium diameter 1.54 mm. with 7 to 12 major septa (East Ogwell sample). Septa rarely slightly dilated at tabularium boundary. Dissepiments characteristically weakly arched and rather elongate; flattened horseshoes extremely rare. Tabularium structure simple.

LECTOTYPE. Selected by Soshkina (1951 : 89). The original of Edwards & Haime's (1853, pl. 55), figs. 2, 2a. Devonian; Torquay, south Devon. This specimen appears to be lost.

MATERIAL. Ramsleigh Quarry: TM(JB)294a (Colony 1), TM136/7 (Colony 2). Other measured specimens: BM(NH) R46372-73.

DISTRIBUTION. England: Lower Frasnian limestones, Ramsleigh Quarry, East Ogwell, near Newton Abbot, south Devon. Also Frasnian of Germany (Harz) and ? the U.S.S.R. (southern Urals).

DESCRIPTION. The material is fragmentary and nothing is known of the external features, shape and overall size of the corallum.

The colony is thamnasterioid, with the septa of adjacent corallites most commonly perfectly confluent and less frequently irregularly abutting. Occasional septa may have free ends in the dissepimentarium. The tabularia are regularly and fairly widely spaced.

The septa are 0.05-0.1 mm. thick and are regularly developed between tabularia. They may be straight, but are usually sinuous and occasionally geniculate. In some cases, the sides of the septa are slightly corrugated, presumably by the presence of slightly swollen trabeculae; they are never truly carinate and usually the septa are smooth sided. Septal dilatation at the tabularium boundary is slight or lacking. Usually the major septa project into the tabularium for between 0.1 and 0.2 mm. with no change in thickness. At this point, they thin abruptly and continue towards the axis as strongly attenuate filaments. Occasionally the major septa reach the axis but more commonly, they either curve sharply to become confluent with an adjacent or nearby septum, or they end about a third of the tabularium radius short of the axis. The minor septa end at the tabularium junction.

The dissepiments are uniserial between adjacent septa. The tabularium junction is strongly and sharply defined.

In longitudinal-section, the dissepimentarium is composed of several series of elongate, weakly arched vesicles. The dissepiments are very uniformly developed with a height of 0.1 mm. The surface of the dissepimentarium is flat peripherally, rising slightly to a crest just outside the tabularium junction. Rarely a flattened horseshoe dissepiment may occur among the series forming the crest, whilst on the tabularium side, a vertically discontinuous row of normal dissepiments slopes steeply axially and downwards.

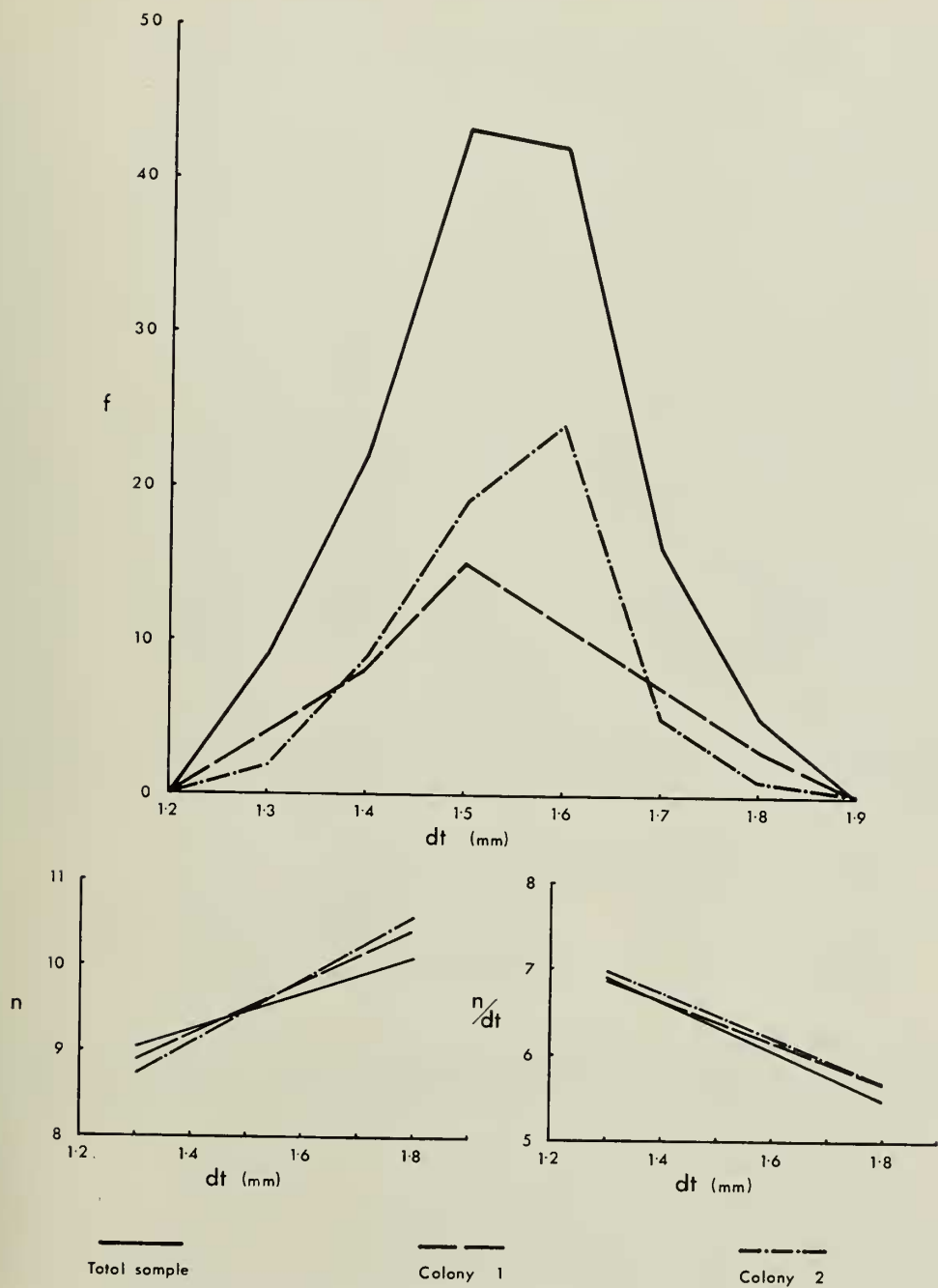
FIG. 19. *Frechastraea bowerbanki*.

TABLE 12.—Statistical data for some characters of *Frecheastraea bowerbanki*.

		Total sample	Colony 1	Colony 2
	N	137 (4)	48	60
dt	O.R.	1.3-1.8	1.3-1.8	1.3-1.8
	$\bar{x}$	1.54	1.54	1.54
	s	0.12	0.13	0.10
	C.V.	7.73	8.65	6.56
	S.E. _m	0.010	0.019	0.013
n	O.R.	7-12	8-11	7-12
	$\bar{x}$	9.54	9.65	9.62
	s	0.25	0.42	0.37
	C.V.	2.59	4.31	3.89
	S.E. _m	0.021	0.060	0.048
n/dt	O.R.	4.71-7.69	5.00-7.14	5.00-7.14
	$\bar{x}$	6.24	6.30	6.36
	s	0.34	0.32	0.26
	C.V.	5.48	5.06	4.09
	S.E. _m	0.029	0.046	0.034

Graphs:—

n/dt	r	0.89	0.86	0.86
	a	2.08	3.13	3.70
	b	6.34	4.84	3.91
n/dt / dt	r	-0.99	-0.95	-0.77
	a	-2.88	-2.40	-2.57
	b	10.66	9.99	10.32

	A	At	At/A	Graph:—At/A	
O.R.	0.29-0.38	0.016-0.020	0.050-0.057	r	0.96
$\bar{x}$	0.34	0.018	0.054	a	0.036
s	0.043	0.0015	0.0033	b	0.0062
C.V.	12.56	8.34	6.13		
S.E. _m	0.021	0.00077	0.0017		

Tabularium structure is simple and is formed with both complete and incomplete tabulae. The complete plates are saucer-shaped, whilst the incomplete plates are flat to slightly arched vesicles, horizontally disposed in the centre of the tabularium and sloping steeply downwards periaxially. The vertical spacing of the tabulae varies considerably between 0.05 and 0.3 mm.

Increase is lateral, with the daughter corallites developing in the dissepimental tissue equidistant from the surrounding adult tabularia.

Only four incomplete colonies from Ramsleigh Quarry were available for analysis, two of which have been selected for individual treatment. The statistics are listed in Table 12 and illustrated graphically in Text-figs. 16 and 19.

DISCUSSION. Although the lectotype is lost, there can be no doubt from Edwards & Haime's (1853 : 241, pl. 55, figs. 2, 2a) description and figures, of the interpretation of this species. Figure 2a shows clearly the distinctive characters in cross-section which have been described in the present material. Furthermore, they state (1853 : 242) that the diameter of the 'wall' (= tabularium diameter) is about two-thirds of a line, which is approximately 1.4 mm. This agrees with the present observations but contrasts with the measurements given by Rózkowska (1953 : 67) for her *Phillipsastraea bowerbanki*. Rózkowska's specimen is, in fact, distinct from the present species and belongs to *Frechastraea pentagona minima* (see p. 240).

Quenstedt (1852 : 664, pl. 60, fig. 3) erected a new species, *Acervularia seriaca*, which from his figure and description appears to be conspecific with *F. bowerbanki*. Frech (1885 : 63) was of the same opinion and placed Quenstedt's species in the synonymy for his *Phillipsastrea bowerbanki*. Later Quenstedt (1879 : 536, pl. 163, fig. 1) refigured *Acervularia seriaca* and in the same work (p. 536, pl. 162, fig. 39) also described and figured '*Smithia bowerbanki* Edwards and Haime'. On the evidence of the figures, the specimen of *Acervularia seriaca* appears, as before, to belong to the present species, whilst his *Smithia bowerbanki* is probably referable to *F. pentagona minima*.

F. bowerbanki differs greatly from the species of *Frechastraea* described above. This species has tabularia corresponding in size to those of *F. goldfussi* but the number of septa at any given diameter is strikingly lower in the former. *F. bowerbanki* also occupies a distinctive position on the graph of tabularium area plotted against corallite area, reflecting the relatively wide spacing of the tabularia (Text-fig. 16, Table 10).

F. bowerbanki is further distinguished by its thamnasterioid form and particularly by weakly arched, rather elongate dissepiments in contrast to the globose dissepiments usually found in species of *Frechastraea*.

Genus *THAMNOPHYLLUM* Penecke 1894

- 1894 *Thamnophyllum* Penecke : 563.
- 1909 *Phacellophyllum* Gürich : 102.
- 1935 *Disphyllum* {*Phacellophyllum*}; Lang & Smith : 546.
- 1935 *Thamnophyllum*; Lang & Smith : 563.
- 1939 *Disphyllum* {*Phacellophyllum*}; Hill : 224.
- 1939 *Thamnophyllum*; Hill : 227.
- partim 1940 *Thamnophyllum*; Hill : 260.
- 1940 *Phacellophyllum*; Lang, Smith & Thomas : 98.
- 1940 *Thamnophyllum*; Lang, Smith & Thomas : 133.
- 1949 *Phacellophyllum*; Stumm : 36.
- 1949 *Thamnophyllum*; Stumm : 36.
- partim 1949 *Macgeea* (*Thamnophyllum*); Schouppé : 100.
- 1949 *Thamnophyllum*; Soshkina : 77.
- partim 1950 *Phacellophyllum* (*Phacellophyllum*); Wang : 219.
- 1950 *Phacellophyllum* (*Thamnophyllum*); Wang : 219.
- 1951 *Disphyllum* {*Phacellophyllum*}; Taylor : 185.
- 1951 *Thamnophyllum*; Soshkina : 74.
- 1952 *Thamnophyllum*; Soshkina : 85.

- 1953 *Thamnophyllum*; Rózkowska : 13.
 partim 1953 *Macgeea*; Rózkowska : 18.
 1954a *Phacellophyllum*; Hill : 26.
 1954 *Thamnophyllum*; Soshkina : 65.
 1956 *Thamnophyllum*; Rózkowska : 304.
 1956a *Macgeea* (*Thamnophyllum*); Flügel : 48.
 partim 1956a *Macgeea* (*Macgeea*); Flügel : 53.
 1956b *Macgeea* (*Thamnophyllum*); Flügel : 361.
 partim 1956b *Macgeea* (*Macgeea*); Flügel : 361.
 1956 *Thamnophyllum*; Hill : 281.
 1956 *Phacellophyllum*; Hill : 282.
 1957 *Thamnophyllum*; Rózkowska : 83.
 1958 *Macgeea* (*Thamnophyllum*); Flügel : 625.
 1958 *Macgeea* (*Thamnophyllum*); Schouppé : 226.
 1959 *Thamnophyllum*; Flügel : 115.
 partim 1959 *Phacellophyllum*; McLaren : 28.
 1960 *Thamnophyllum*; Rózkowska : 44.
 partim 1963 *Macgeea* (*Macgeea*); Schouppé & Stacul : 288.
 1963 *Macgeea* (*Thamnophyllum*); Schouppé & Stacul : 291.
 1964 *Thamnophyllum*; Webby : 9.

DIAGNOSIS. Dendroid or phaceloid rugose corals with axial and in one species, lateral increase. Septa of two orders, usually spindle-shaped in dissepimentarium. Dissepimentarium typically with outer series of flat dissepiments and inner series of horseshoe dissepiments. In some species, dissepimental structure obscured by stereoplastic thickening. Tabulae complete or incomplete, with periaxial plates variably developed.

TYPE SPECIES. Selected by Lang & Smith (1935 : 564) and see Flügel (1958 : 625). *Thamnophyllum stachei* Penecke 1894 : 594, pl. 8, figs. 1-3; pl. 11, figs. 1, 2. Emsian (*barrandei*-Schichten); Marmorbruch am Graz, Austria.

DISTRIBUTION. Lower to Upper Devonian of Europe, Asia, Australia and North America.

DISCUSSION. Penecke (1894 : 563) described four species of *Thamnophyllum*, three of them new and the other *T. trigeminum* (Quenstedt) (see *T. germanicum germanicum* nom. nov., p. 260). From these, Lang & Smith (1935 : 564) selected *T. stachei* as type species and redescribed this and Penecke's other species. They removed *T. trigeminum* from *Thamnophyllum* and assigned it to *Phacellophyllum* Gürich, which they regarded as a genomorph of *Disphyllum*. Gürich (1909 : 102) had placed only '*Phacellophyllum caespitosum* Goldf.' in his new genus. As Lang & Smith (1935 : 547) pointed out, Gürich's figures (1909, pl. 31, figs. 5a, b) were copied from Schlüter (1881, pl. 9, figs. 6, 7) which fixes the type species of *Phacellophyllum* as *Lithodendron caespitosum* Goldfuss.

Schouppé (1949), in a detailed consideration of species of *Thamnophyllum* and *Phacellophyllum*, was the first to place the latter in synonymy with the former. Furthermore, he made *Thamnophyllum* a subgenus of *Macgeea* on the basis of their similar structural plan, separating *M. (Thamnophyllum)* and *M. (Macgeea)* principally on their growth form.

Both Soshkina (1951, 1952, 1954) and Rózkowska (1953, 1956, 1957, 1960) followed

Schouppé in considering *Phacellophyllum* as synonymous with *Thamnophyllum*, but neither supported the subgeneric relationship with *Macgeea*: Rózkowska (1953 : 18, 1957 : 102) listed the characters by which *Macgeea* and *Thamnophyllum* may be distinguished. On the other hand, Hill (1954a, 1956) and McLaren (1959) retained *Thamnophyllum* and *Phacellophyllum* as separate genera. McLaren (1959 : 28) pointed out that *T. stachei*, type species of *Thamnophyllum*, is imperfectly known, whereas *Phacellophyllum* has adequately described type material. From Lang & Smith's (1935) descriptions, he regarded the synonymy of the two genera as by no means certain.

The development of periaxial tabulae in the type species of *Phacellophyllum* has led to an involved and lengthy exchange on the taxonomic position of this genus in recent years between Flügel and Schouppé. Flügel (1956a : 53, 1965b : 361), describing the peripheral plates in the tabularium of *Lithodendron caespitosum* as a third zone of normal dissepiments, compared the structure of the species in longitudinal-section with that developed in typical forms of *Macgeea*. On this basis, he placed *Phacellophyllum* in synonymy with *Macgeea sensu stricto* and retained *Thamnophyllum* as a subgenus of *Macgeea* characterized by only two zones of dissepiments, flat and horseshoe. Schouppé (1958 : 220 *et seq.*) rejected this classification. He considered the 'third dissepimental zone' to constitute part of the tabularium structure and stated (p. 227) that no sharp line could be drawn between the development of periaxial tabulae in *Macgeea* and *Thamnophyllum*. Schouppé thus retained his 1949 classification, placing *Phacellophyllum* in *Thamnophyllum*, which he separated subgenerically from *Macgeea* on the basis of their contrasting growth form and grade of general structural complexity. Flügel (1959 : 115, footnote) later criticized Schouppé's (1958) subgeneric diagnoses as insufficiently differentiated. Nevertheless, he subscribed to a very similar classification, that of Rózkowska (1957), considering not only *Phacellophyllum* to be synonymous with *Thamnophyllum*, but the latter to be generically distinct from *Macgeea*. Finally, Schouppé & Stacul (1963) published a detailed consideration of the genera involved, in which they returned almost exactly to the position held by Flügel (1956). They wrote (1963 : 285) that '... the principal stress in the systematic classification should be laid on the appearance of vesicular elements in the peripheral area of the tabularium. Consequently, all those forms having peripheral vesicles in the tabularium (even if only sporadic...) must be placed in *Macgeea* (*Macgeea*). Forms with, on the other hand, simple, peripheral, 'split-open' tabulae or additional periaxial, sloping, plate-like elements—without peripheral vesicles—belong to *Macgeea* (*Thamnophyllum*).' Thus they placed *Phacellophyllum* in synonymy with *Macgeea* (*Macgeea*).

In the writer's opinion, *Phacellophyllum* is a junior synonym of *Thamnophyllum* and the latter is generically distinct from *Macgeea*. The periaxial elements, so conspicuous in some specimens of *Lithodendron caespitosum* may show considerable variation in their development within the species as a whole (see p. 268). Furthermore, they occur to a greater or lesser degree in many other species of *Thamnophyllum*. It seems unreasonable to suggest a morphological and genetic distinction between the periaxial elements developed in *Phacellophyllum* and *Thamnophyllum* at what must be considered an arbitrary level in their degree of structural complexity. Such

a variable character cannot be used as the basis of a subgeneric division, especially as it cuts across the more obvious distinction in growth form. Species of *Macgeea* are simple, conical corals which only rarely show budding. In a collection of 234 individuals belonging to six species and subspecies, Rózkowska (1957 : 118) found only four budding specimens. *Thamnophyllum* and *Phacellophyllum*, on the other hand, are phaceloid or dendroid forms with cylindrical corallites. Commonly in *Macgeea*, the horseshoe dissepiments are less regular in form and superposition with a generally more complex tabularium and dissepimentarium structure. In addition, *Macgeea* usually shows distinct bilateral symmetry in the adult stage in contrast to the radial symmetry of *Thamnophyllum* and *Phacellophyllum*.

As McLaren (1959 : 28) remarked, existing knowledge of *T. stachei* is rather imperfect, but the writer believes enough is known from the work of Lang & Smith (1935 : 581) to permit an opinion on the taxonomic status of *Thamnophyllum*. *T. stachei*, from Penecke's figures, Lang & Smith's description and their specimens (BM(NH) R30990-94), shows evidence of all the characteristic features described in better known species of *Thamnophyllum*. As Rózkowska (1957 : 101) stated, it is a primitive early member of the genus in which the tabulae are very simple and widely spaced. Stereoplastic thickening, which in *T. stachei* almost completely obscures the dissepimental structure, is also a variable factor in other species of *Thamnophyllum*.

***Thamnophyllum germanicum germanicum* nom. nov.**

- 1894 *Thamnophyllum trigeminum* (Quenstedt) Penecke : 596, pl. 8, figs. 4-6.
 1959 *Thamnophyllum trigeminum trigeminum* Penecke; Flügel : 117 (see for extensive synonymy).
 1960 *Thamnophyllum trigeminum trigeminum* Penecke; Rózkowska : 53.
 1963 *Macgeea* (*Thamnophyllum*) *trigemina trigemina* (Penecke) Schouppé & Stacul, text-figs. 5, ?19.
 1963 *Macgeea* (*Macgeea*) sp. Schouppé & Stacul, text-fig. 18.

But not :

- 1879 *Cyathophyllum caespitosum trigemme* Quenstedt : 518, pl. 162, figs. 5-8.

DIAGNOSIS. See Rózkowska (1956 : 310).

LECTOTYPE. Selected by Flügel (1959 : 118). UPG 891 (Collections of the Paläontologisches Institut, Graz) labelled by Penecke in 1892 as "*Fascicularia trigemina*". Givetian; (?) Auberger, near Gerolstein, Eifel, Germany.

DESCRIPTION. See Rózkowska (1956 : 310).

DISCUSSION. *Cyathophyllum caespitosum trigemme* Quenstedt has been shown by Flügel (1959) to belong to *Favistella* (*Dendrostella*). Hitherto it had been regarded as a species of *Thamnophyllum*, largely due to Penecke (1894 : 596) misinterpreting Quenstedt's description and illustrating as *Thamnophyllum trigeminum* (Quenstedt) a new and generically different species. Subsequent workers had relied mainly on Penecke's work for the identification of Quenstedt's subspecies.

Flügel (1959 : 117) thus described Penecke's material as *Thamnophyllum trigeminum trigeminum* Penecke. The retention of Quenstedt's specific name for Penecke's misidentified material, however, is not in accordance with Article 49 of the I.C.Z.N.

(1964) and a new name is required. With the permission of Professor Flügel, *Thamnophyllum trigeminum trigeminum* Penecke is hereby renamed *Thamnophyllum germanicum germanicum* nom. nov. after the country of origin of Penecke's specimens.

***Thamnophyllum germanicum schouppéi* nom. nov.**

Plate 13, figs. 1-4; Plate 14, figs. 1-4

1949 *Macgeea* (*Thamnophyllum*) *caespitosa* (Goldfuss) var. *minus* (F. A. Roemer) Schouppé : 152
pars, pl. 10, figs. 21-24; pl. 13, figs. 73-75 (*non* pl. 11, figs. 38-39; pl. 13, figs. 76-77;
 pl. 14, figs. 100a-c).

1956b *Macgeea* (*Thamnophyllum*) *minima* Schouppé, Flügel : 361.

1965 *Thamnophyllum* cf. *trigeminum* Penecke; Scrutton : 186.

But not:

1855 *Diphyphyllum minus* F. A. Roemer : 29, pl. 6, figs. 12a-c.

DIAGNOSIS. *Thamnophyllum* with mean corallite diameter 4.2 mm. and 12 to 20 major septa (topotype sample). Axial increase with three or four buds lacking caenogenetic tissue in axils of branches. Tabulae complete or incomplete with periaxial plates sporadically developed. Skeletal elements generally unthickened.

HOLOTYPE. See Flügel (1956b : 361). UGP327 (Collections of the Paläontologisch Institut, Graz). The specimen is labelled "Middle Devonian, Torquay" only, but it comes without doubt from the Givetian limestones in Dyer's Quarry.

MATERIAL. Dyer's Quarry: OUM D506 (Colony 1), OUM D507 (Colony 2), OUM D508 (Colony 3). Other measured material: OUM D271, OUM D509, OUM D511. Additional material: OUM D272, OUM D504-5, OUM D510.

DISTRIBUTION. Type locality only.

DESCRIPTION. Colonies are phaceloid, up to 100 cm. in diameter, consisting of close-spaced, sub-parallel, cylindrical corallites. External features are unknown as recent weathering has removed the epitheca to expose the peripheral ends of the septa. Calices have not been observed.

In cross-section the corallites are circular to sub-circular. The epitheca, normally about 0.1 mm. thick, is frequently preserved within the matrix. The septa, of two orders, are slightly spindle-shaped in the dissepimentarium. The minor septa may or may not penetrate very slightly into the tabularium but the major septa usually reach a half to two-thirds the distance to the axis. The septa are normally straight in the dissepimentarium but the major septa often become slightly curved or sinuous in the tabularium.

The traces of the sides of the horseshoe dissepiments form a distinctive double wall in cross-section. Between adjacent septa, the two walls are convex towards each other, reflecting the saddle-shaped form of the horseshoe dissepiments. They are, on average, about 0.4 mm. apart, with the outer wall the same distance from the epitheca. The innermost wall is the boundary between the dissepimentarium and the tabularium.

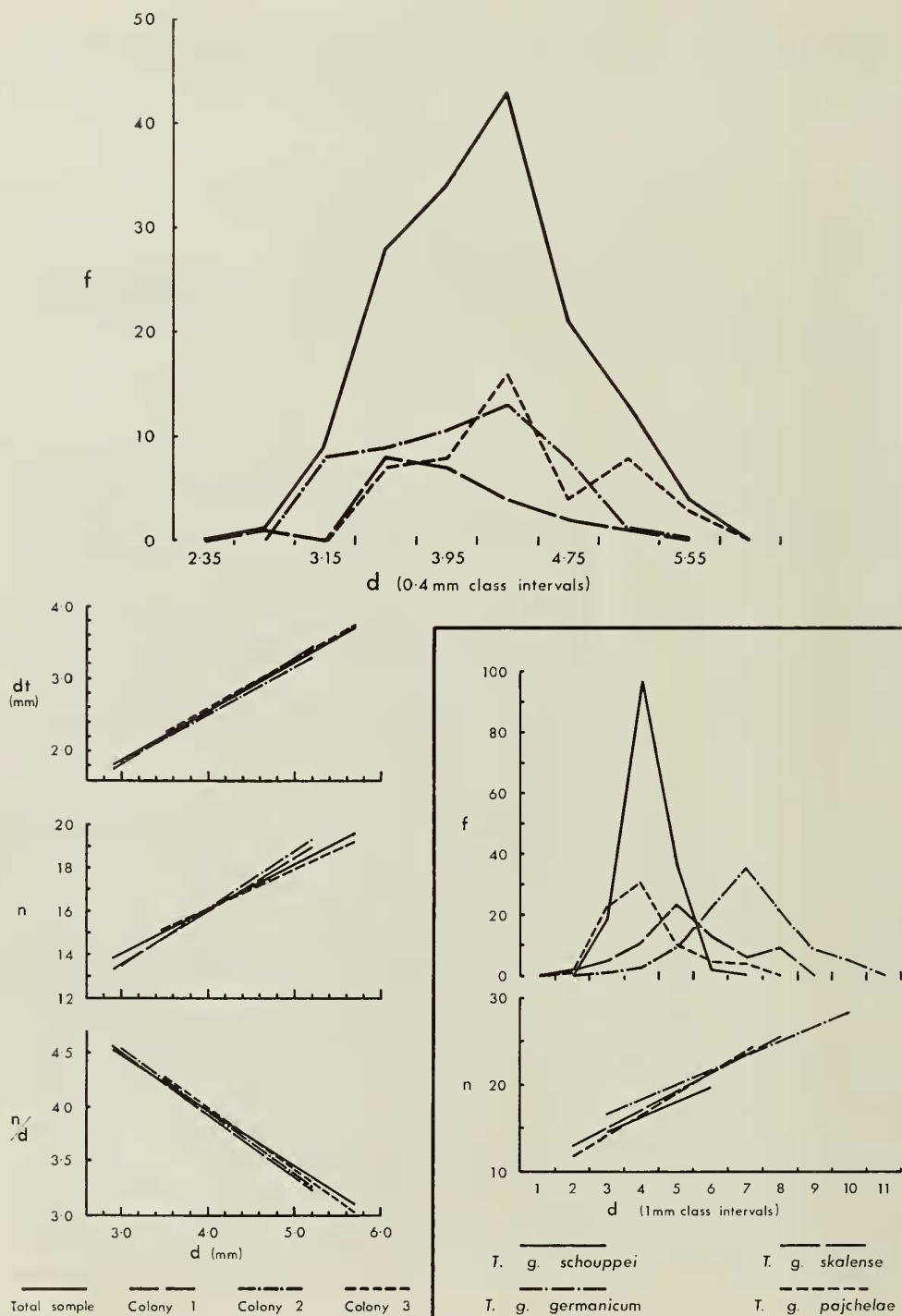


FIG. 20. *Thamnophyllum germanicum schouppaei*. Inset: Graphical comparison of some quantitative characters for the subspecies of *Thamnophyllum germanicum*.

In longitudinal-section, the dissepimentarium is composed of an outer series of flat plates and an inner series of horseshoe dissepiments. The outer plates are not always seen as they are easily removed by erosion. They are slightly irregular in spacing, usually between 0.2 and 0.5 mm. apart and always uniserial. They may be perfectly flat, slightly concave or convex. The horseshoe dissepiments are thin walled and regularly developed in a single series, normally between three and four to 1 mm.

The tabulae are complete or incomplete, often with irregularly developed periaxial plates. They may be flat or slightly bowed or arched, and sometimes strongly convex towards the calice. Tabulae in the form of flat-topped domes are rare. The spacing of the tabulae is variable but averages about 18 to 1 cm.

Increase is exclusively axial with three or four daughter corallites produced in each case. There is no indication of extra-dissepimental tissue (caenogenetic tissue of Soshkina 1953) between the newly formed buds. As soon as normal dissepimental tissue begins to form in the axial area of the parent corallite, the daughter corallites become phaceloid.

Increase is often seen in hand specimen but it is difficult to assess quantitatively the frequency with which it occurs. On one specimen, OUM D508/4, three newly formed corallites were seen to bud themselves. The increments of vertical growth between formation and budding in these cases measured 1.3 cm., 1.4 cm. and 1.7 cm. Also the corallite diameters at which budding may occur are usually indeterminate as it is very rare to obtain a cross-section at the inception of blastogeny when it is still possible to measure the diameter of the parent corallite.

A statistical analysis has been made of a total sample comprising six colonies from Dyer's quarry. Three of these colonies have also been analysed individually. The statistics are listed in Table 13 and illustrated graphically in Text-fig. 20.

DISCUSSION. Specimen UPG327 was first described, with some other material, as *Macgeea* (*Thamnophyllum*) *caespitosa* var. *minus* (F. A. Roemer) by Schouppé (1949 : 152). Both Flügel (1965*b* (August) : 361) and Schouppé (1956 (September) : 153, footnote) noted that the Torquay specimen was not in fact conspecific with Roemer's species and Flügel suggested that, as a species in its own right, it should be called *Macgeea* (*Thamnophyllum*) *minima* Schouppé. Under article 49 (Article 70*b* does not apply here) of the I.C.Z.N. (1964), however, Flügel's use of Roemer's specific name for Schouppé's misidentified material is invalid and a new name is needed. With the permission of Professors A. von Schouppé and H. Flügel, "*Macgeea* (*Thamnophyllum*) *minima* Schouppé" is hereby renamed, as a subspecies of *Thamnophyllum germanicum*, *T. germanicum schouppéi* nom. nov.

In his original description, Schouppé (1949 : 155) stated that 'The budding is lateral and not parricidal (= axial)' in *Macgeea* (*Thamnophyllum*) *caespitosum* var. *minus*. This is certainly true of Roemer's species and Schouppé's remark must have been based on correctly identified material. The holotype, in fact, gives no clear indication of its style of increase, although the evidence from topotypic material of the present subspecies shows that it must be axial.

Thamnophyllum germanicum schouppéi is closest in general characteristics to the other subspecies of *T. germanicum* described from the Middle Devonian—*T. ger-*

manicum germanicum nom. nov., *T. germanicum skalense* (Rózkowska) and *T. germanicum pajchela* (Rózkowska) (see Rózkowska 1960: 53). As Rózkowska (1956) gave data on corallite diameter and number of major septa for the latter three subspecies, it is possible to compare them statistically with the present material

TABLE 13.—Statistical data for some characters of *Thamnophyllum germanicum schoupppei*.

	N	Total sample 153	Colony 1 23	Colony 2 50	Colony 3 46
d	O.R.	2.9-5.7	2.9-5.2	3.0-5.2	3.5-5.7
	$\bar{x}$	4.19	3.94	4.00	4.42
	s	0.59	0.51	0.56	0.59
	C.V.	14.08	12.82	13.98	13.35
	S.E. _m	0.048	0.11	0.079	0.082
dt	O.R.	1.7-3.7	1.7-3.3	1.8-3.1	2.1-3.7
	$\bar{x}$	2.69	2.52	2.53	2.84
	s	0.40	0.37	0.36	0.39
	C.V.	14.79	14.51	14.18	13.80
	S.E. _m	0.032	0.076	0.051	0.058
dt/d	O.R.	0.55-0.70	0.59-0.70	0.55-0.65	0.62-0.69
	$\bar{x}$	0.64	0.64	0.63	0.65
	s	0.016	0.023	0.020	0.021
	C.V.	2.43	3.63	3.09	3.30
	S.E. _m	0.0013	0.0048	0.0028	0.0031
n	O.R.	12-20	13-18	12-20	13-20
	$\bar{x}$	16.52	15.91	16.14	16.84
	s	1.22	1.24	1.51	1.09
	C.V.	7.41	7.77	9.35	6.44
	S.E. _m	0.099	0.26	0.21	0.16
n/d	O.R.	3.08-5.16	3.41-5.00	3.46-5.16	3.08-4.77
	$\bar{x}$	3.98	4.07	4.06	3.85
	s	0.30	0.29	0.31	0.34
	C.V.	7.51	7.00	7.72	8.78
	S.E. _m	0.024	0.059	0.044	0.050
Graphs:—					
dt/d	r	0.99	0.96	0.98	0.98
	a	0.68	0.73	0.64	0.66
	b	-0.14	-0.34	-0.036	-0.094
n/d	r	0.90	0.85	0.85	0.78
	a	2.08	2.45	2.70	1.84
	b	7.83	6.26	5.34	8.71
n/d / d	r	-0.94	-0.84	-0.78	-0.90
	a	-0.51	-0.56	-0.56	-0.57
	b	6.11	6.29	6.30	6.38

(Table 14 and Text-fig. 20). Only *T. germanicum pajchela* proved not to be significantly different from *T. germanicum schoupppei* in the frequency distribution of their corallite diameters. When septal number was plotted against corallite diameter, however, the lines of all three subspecies were found to be significantly different from that for *T. germanicum schoupppei*.

Qualitatively, the latter differs from the other three subspecies by the absence of caenogenetic tissue between newly formed buds. *T. germanicum skalense* also differs through the excessive thickening of its septa in the zone of horseshoe dissepiments and *T. germanicum pajchela* is remarkable for its regular and widely spaced complete tabulae and general simplification of its internal structure.

T. germanicum schoupppei differs markedly from the Frasnian subspecies of *Thamnophyllum germanicum*, *T. germanicum kozlowskii* (Różkowska) and *T. germanicum superius* (Różkowska) (see Różkowska 1960 : 53), through the larger dimensions of the latter pair. The mean corallite diameters of the Frasnian subspecies (Różkowska 1957 : 93 as *T. kozlowskii* and *T. kozlowskii superius*) are 10.03 and 9.28 mm. respectively. In addition, *T. germanicum kozlowskii* is characterized by a more complex dissepimentarium than typical thamnophyllids, with one or two series of horseshoe dissepiments, and the tabularium has highly developed periaxial elements. In the writer's opinion, this form deserves full specific rank. *T. germanicum superius*,

TABLE 14.—Statistical discrimination between some characters of *Thamnophyllum germanicum* subspecies and *T. germanicum schoupppei*. Significant values in bold.

		<i>schoupppei</i>	<i>pajchela</i>	<i>skalense</i>	<i>germanicum</i>
	N	153	73	69	107
	O.R.	3-6	2-7	2-8	3-10
d	$\bar{x}$	4.14	4.11	5.36	7.00
	s	0.62	1.13	1.52	1.39
	C.V.	15.01	27.37	28.42	20.81
	S.E. _m	0.050	0.13	0.18	0.13
"t" test against <i>schoupppei</i> :—					
	t		0.29	8.46	22.45
n	O.R.	12-20	12-25	10-27	16-29
	$\bar{x}$	16.53	16.90	20.01	23.25
	s	1.06	2.81	3.21	2.34
	C.V.	6.43	16.60	16.04	10.07
	S.E. _m	0.086	0.33	0.39	0.23
Graph :—					
n/d	r	0.97	0.99	0.98	1.00
	a	1.71	2.49	2.11	1.69
	b	9.45	6.65	8.72	11.43
"z" test against <i>schoupppei</i> :—					
	z (slope)		13.07	6.00	0.58
	z (position)				19.07

described originally as *T. monozonatum* Soshkina by Rózkowska (1953 : 14), differs from *T. germanicum schoupppei* by the possession of complete, concave tabulae more reminiscent of *T. hornesi* Penecke (as noted by Rózkowska) than the *T. germanicum* group.

T. germanicum schoupppei is closely similar in most respects to *T. caespitosum* (Goldfuss). The latter, however, has exclusively lateral increase in contrast to the axial increase of the former.

Thamnophyllum caespitosum (Goldfuss) *sensu lato*

Plate 15, figs. 2-4; Plate 16, figs. 1, 2

- 1826 *Lithodendron caespitosum* Goldfuss : 44, pl. 13, fig. 4.
- 1848 *Cladocora antiqua* Bronn : 303.
- 1851 *Lithostrotion antiquum* (Bronn) Edwards & Haime : 439.
- 1879 *Cyathophyllum caespitosum* Goldfuss; Quenstedt : 509 *pars*.
- 1881 *Fascicularia caespitosa* (Goldfuss) Schlüter : 103, pl. 9, figs. 6, 7.
- 1885 *Cyathophyllum caespitosum* Goldfuss; Frech : 33 *pars*.
- 1909 *Phacellophyllum caespitosum* (Goldfuss) Gürich : 102 *pars*, pl. 31, fig. 5.
- 1935 *Disphyllum* {*Phacellophyllum*} *caespitosum* (Goldfuss) Lang & Smith : 573, *pars*, text-figs. 28, 29, pl. 35, figs. 1, 2.
- 1949 *Macgeea* (*Thamnophyllum*) *caespitosa* (Goldfuss) Schouppé : 138, pl. 9, fig. 3, pl. 11, figs. 40-43.
- 1949 *Phacellophyllum caespitosum* (Goldfuss); Stumm : 36, pl. 17, figs. 11-13.
- 1951 *Disphyllum* {*Phacellophyllum*} *caespitosum* (Goldfuss); Taylor : 186, pl. 3, figs. 3a, b, non figs. 4a, b.
- 1956 *Thamnophyllum caespitosum* (Goldfuss); Rózkowska : 308, text-figs. 30-32.
- 1956a *Macgeea* (*Macgeea*) *caespitosa* (Goldfuss) Flügel : 54.
- 1956b *Macgeea* (*Macgeea*) *caespitosa* (Goldfuss); Flügel : 361.
- 1957 *Thamnophyllum caespitosum* (Goldfuss); Rózkowska : 89, text-fig. 8.
- 1958 *Macgeea* (*Thamnophyllum*) *caespitosum* (Goldfuss); Schouppé : 227, text-figs. 7-9.
- 1963 *Macgeea* (*Macgeea*) *caespitosa* (Goldfuss); Schouppé & Stacul : 268, text-figs. 4, 17.
- 1964 *Thamnophyllum caespitosum* (Goldfuss); Webby : 9, text-figs. 3a-d.

But not:

- 1826 *Cyathophyllum caespitosum* Goldfuss : 60, pl. 19, figs. 2a-d.
- 1956 *Phacellophyllum caespitosum* (Goldfuss); Hill : 282, text-fig. 192 (6).

DIAGNOSIS. Phaceloid *Thamnophyllum*. Mean tabularium diameter 6.17 mm. with 18 to 22 major septa (Wolborough Quarry sample). Major and minor septa slightly dilated in zone of horseshoe dissepiments. Dissepimentarium regularly developed with single outer series of horizontal plates and single inner series of horseshoe dissepiments with slightly thickened sides. Tabularium structure highly variable from closely spaced flat-topped domes with inosculating periaxial tabulae to complete, sagging plates, well spaced and with rare subsidiary plates. Increase lateral.

LECTOTYPE (selected by Lang & Smith 1935 : 573). Original of Goldfuss 1826, pl. 13, fig. 4 (Goldfuss Collection, Geologisch-Paläontologisches Institut, Bonn). Givetian; Bensberg, near Köln, Germany.

MATERIAL. BM(NH) R46167-75; middle Givetian limestones, Wolborough Quarry, Newton Abbot, south Devon.

DISTRIBUTION. England: middle and upper Givetian of the Ilfracombe Beds, north Devon and west Somerset; Givetian limestones, Plymouth; middle Givetian limestones of Wolborough Quarry, Newton Abbot, south Devon. Also common in the Givetian of Europe.

DESCRIPTION. Colonies with well spaced, cylindrical corallites. External features and colony shape unknown as the material is fragmented and embedded in a hard, limestone matrix.

In cross-section, the corallites are circular to sub-circular. The epitheca, which is rarely preserved in the matrix, is about 0.05 mm. thick. Major and minor septa are slightly and evenly dilated to 0.1 mm. thickness for a length of 1-1.25 mm. across the zone of horseshoe dissepiments. The minor septa appear to penetrate slightly into the tabularium whilst the major septa, thin and often slightly sinuous, continue towards the axis. The latter are a half to two-thirds the corallite radius in length.

The traces of the horseshoe dissepiments form two strong internal walls, convex towards each other, in cross-section.

In longitudinal-section, the dissepimentarium comprises an outer series of horizontal plates and an inner series of horseshoe dissepiments, their respective widths in the ratio 1 : 1.3. The plates of the outer series may be flat or very slightly curved and are exclusively uniserial. Their spacing varies between 0.25 mm. and 0.65 mm. The horseshoe dissepiments are also exclusively uniserial and fairly uniform in size and shape. They average 0.3 mm. high. The crest of each horseshoe is thin but the sides are moderately and evenly thickened up to 0.01 mm.

The axial tabulae are complete or incomplete, usually closely spaced and arched with a wide flat crest. Periaxial elements are usually well developed as small arched plates inosculating with the main tabulae. Tabularium structure is, however, very variable and includes corallites with wide flat tabulae with scattered periaxial plates and rarely, well spaced, dominantly complete, saucer-shaped tabulae. The vertical spacing of plates in the axis of the tabularium varies from 14 per cm. when the structure is complex, to 10 per cm. when the structure is simple.

Increase, only observed in a few cases, is lateral with a high angle of divergence between parent and bud.

It was possible to measure only a few corallites accurately so that no attempt has been made to analyse the figures in detail. Data obtained are given in Table 15b.

DISCUSSION. See under *Thamnophyllum caespitosum paucitabulatum* (p. 268).

***Thamnophyllum caespitosum paucitabulatum* subsp. nov.**

Plate 15, fig. 1; Plate 16, figs. 3-7; Plate 17, figs. 1-3

DERIVATION OF NAME. The name, *pauci-* (*paucus* L. = few) *tabulatum*, refers to the simple, relatively wide spaced tabulae characteristic of the subspecies.

DIAGNOSIS. *Thamnophyllum caespitosum* with tabularium composed of flat, slightly arched, or saucer-shaped tabulae with rare periaxial elements. Mean tabularium diameter 5.68 mm. with 16 to 21 major septa (Topotype sample).

HOLOTYPE. BM(NH) R46165; upper Givetian limestones; Lummaton Quarry, Torquay, south Devon.

MATERIAL. BM(NH) R46160-6.

DISTRIBUTION. Type locality only.

DESCRIPTION. Subphaceloid colonies of indeterminate size. Corallites cylindrical, subparallel and fairly well spaced. External features are unknown as the material is embedded in a hard limestone matrix.

The structural details are as for *Thamnophyllum caespitosum* above with the following exceptions and additions.

In longitudinal-section, the tabulae are usually complete. They may be slightly arched with wide flat crests, when small arched periaxial elements are poorly developed. More commonly, the tabulae are flat or saucer-shaped with very rare flat or slightly arched subsidiary plates. There are between 8 and 12 tabulae per cm.; spacing of the plates increases from corallites with arched tabulae to those with saucer-shaped tabulae.

Increase is exclusively lateral, occasionally with two offsets developed at the same level. A small amount of extradisseptimental tissue is always developed between the parent and the bud but the angle of divergence is usually high, restricting the plocoid stage to a minimum. Measured corallites showing the early stages of increase are 6.5 and 6.6 mm. in diameter.

A statistical analysis has been made of the sample from Lummaton Quarry. Individual colonies cannot unfortunately be distinguished. The statistics are listed in Table 15a and illustrated graphically in Text-fig. 21a.

DISCUSSION. Previous descriptions of *Thamnophyllum caespitosum* (Lang & Smith 1935 : 573; Rózkowska 1956 : 308; Webby 1964 : 9) all mention tabularia composed of flat or slightly arched tabulae with well developed periaxial elements. No great variation in this structure is mentioned. In fact Flügel (1956b : 361) and Schouppé & Stacul (1963 : 268) have placed this species in *Macgeea* on the basis of the complex tabularium structure (see discussion of *Thamnophyllum*, p. 259). The material collected from Wolborough and Lummaton Quarries in south Devon, however, shows considerable variation in the shape and distribution of the tabulae. The sample from Wolborough has a particularly wide range although the majority of the corallites display the tabularium structure considered typical of *T. caespitosum sensu stricto*. At Lummaton, on the other hand, the typical form is not represented and in most cases the tabularia have wide spaced flat or saucer-shaped tabulae with only rare periaxial elements. Although in other respects the two samples are virtually identical, the range in tabularium structure is so striking and, in view of the taxonomic weight hitherto placed on this character, so important that the erection of a new subspecies, *T. caespitosum paucitabulatum*, for the Lummaton material is felt to be justified.

T. caespitosum caespitosum is interpreted strictly in terms of the lectotype (see Lang & Smith 1935 : 573) and includes the material described by Rózkowska and Webby. The highly variable middle Givetian Wolborough material, however, is

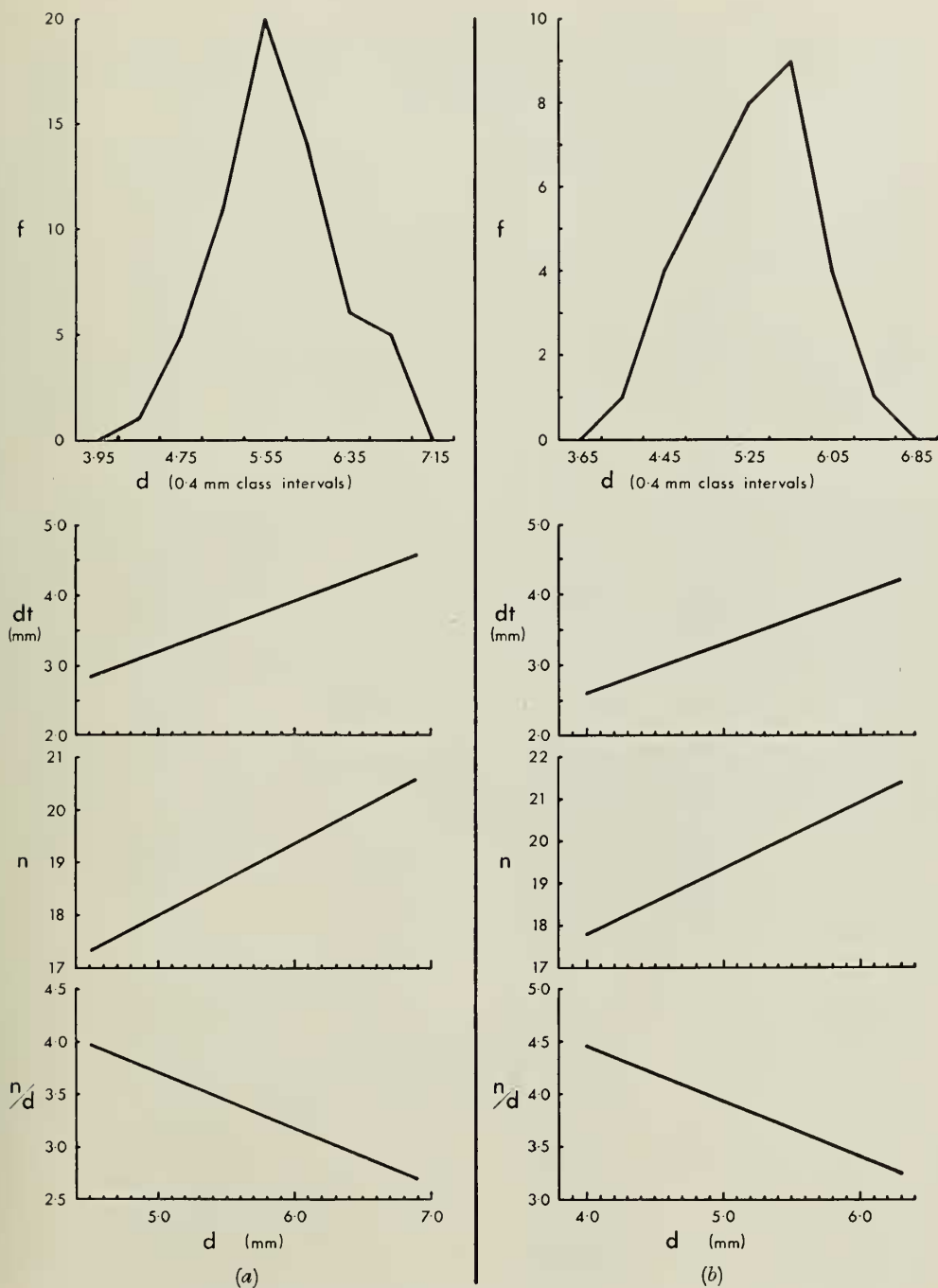
FIG. 21. *a*, *Thamnophyllum caespitosum paucitabulatum*. *b*, *Peneckiella salternensis*.

TABLE 15.—*a*. Statistical data for some characters of *Thamnophyllum caespitosum paucitubulatum*.
b. Statistical data for some characters of *Thamnophyllum caespitosum (sensu lato)*. *c*. Statistical data for some characters of *Peneckiella salternensis*.

		(a)	(b)	(c)
	N	Total sample	Total sample	Total sample
		62	12	33
d	O.R.	4.5-6.9	5.5-7.2	4.0-6.3
	$\bar{x}$	5.68	6.17	5.28
	s	0.55		0.53
	C.V.	9.66		10.11
	S.E. _m	0.070		0.093
dt	O.R.	3.0-4.9	3.5-4.8	2.7-4.3
	$\bar{x}$	3.70	4.14	3.51
	s	0.40		0.38
	C.V.	10.88		10.87
	S.E. _m	0.051		0.066
dt/d	O.R.	0.62-0.71		0.63-0.68
	$\bar{x}$	0.65		0.67
	s	0.021		0.11
	C.V.	3.27		1.68
	S.E. _m	0.0027		0.0020
n	O.R.	16-21	18-22	17-21
	$\bar{x}$	18.92	20.00	19.91
	s	0.75		0.84
	C.V.	3.95		4.21
	S.E. _m	0.095		0.15
n/d	O.R.	2.61-4.26		4.28-3.33
	$\bar{x}$	3.35	3.26	3.80
	s	0.29		0.28
	C.V.	8.78		7.34
	S.E. _m	0.037		0.049
Graphs:—				
dt/d	r	0.95		0.99
	a	0.73		0.72
	b	-0.47		-0.27
n/d	r	0.48		0.81
	a	1.36		1.57
	b	11.19		11.53
n/d /d	r	-0.90		-0.94
	a	-0.54		-0.52
	b	6.40		6.55

assigned to *T. caespitosum sensu lato*, from which it is thought the upper Givetian *T. caespitosum paucitabulatum* from Lummaton directly descended.

Quantitatively, *T. caespitosum paucitabulatum* has a slightly lower mean corallite diameter than that for *T. caespitosum sensu lato* although the latter has insufficient measurements for accurate comparison (Tables 15a, b). Figures available for *T. caespitosum caespitosum*—‘close to 6 mm.’ corallite diameter with ‘usually 18 to 19’ major septa (Webby 1963 : 10) and ‘corallites average about 6 mm. in diameter and have about 20 major septa’ (Rózkowska 1956 : 308)—compare closely with those for the Wolborough material. Lang & Smith (1953 : 574), however, record fewer major septa—16 to 18—with an average corallite diameter of 6 cm. (*sic*) in the lectotype of *T. caespitosum caespitosum*.

T. caespitosum is structurally most similar to the *T. germanicum* group but is distinguished from it, and all other species of *Thamnophyllum*, by the possession of lateral budding.

Thamnophyllum spp.

MATERIAL. BM(NH) R46181, middle Givetian limestones (see Middleton 1959), Shinner’s Bridge Quarry, near Dartington (SX 78906225); BM(NH) R46178, Givetian limestones, road cutting immediately south of junction of Babbacombe Road with Acre Lane, Torquay (SX 93186477); BM(NH) R46177, Givetian limestones, disused quarry on Teignmouth Road, Torquay (SX 91126553); BM(NH) R46179–80, Middle Devonian (?Givetian) thin bedded limestones, 80 ft. above sea level in cliff at northern end of Redgate Beach, Torquay (SX 93516494). All south Devon.

DISCUSSION. These fragments, which do not all belong to the same species or subspecies, can nevertheless be placed in either *Thamnophyllum caespitosum* or *T. germanicum*. Unfortunately none of them gives evidence of the mode of increase which is critical in distinguishing between the two species. Further material may eventually enable the accurate determination of these specimens.

Genus *PENECKIELLA* Soshkina 1939

- partim* 1939 *Peneckiella* Soshkina : 23.
- partim* 1939 *Disphyllum*; Hill : 224.
- partim* 1949 *Peneckiella*; Soshkina : 141.
- partim* 1949 *Macgea* (*Thamnophyllum*); Schouppé : 115.
- partim* 1950 *Phacellophyllum* (*Phacellophyllum*); Wang : 219.
- partim* 1951 *Peneckiella*; Soshkina : 103.
- partim* 1952 *Peneckiella*; Soshkina : 103.
- partim* 1954 *Peneckiella*; Soshkina : 32.
- partim* 1954a *Peneckiella*; Hill : 25.
- 1956 *Peneckiella*; Schouppé : 153.
- 1956a *Peneckiella*; Flügel : 55.
- 1956b *Peneckiella*; Flügel : 355.
- partim* 1956 *Peneckiella*; Hill : 282.
- 1958 *Peneckiella*; Schouppé : 229.
- 1959 *Acinophyllum* McLaren : 22.

- partim* 1959 *Phacellophyllum*; McLaren : 28.
 1960 *Peneckiella*; Rózkowska : 29.
 1960 *Sudetia* Rózkowska : 35.
partim 1965 *Peneckiella*; Strusz : 555.

DIAGNOSIS. Phaceloid or dendroid rugose corals. Septa, major and minor, may be lightly carinate and dilated in dissepimentarium. Characterized by one or two, seldom more, series of dissepiments of variable form but always including peneckieloid dissepiments. Horseshoe, flat and sigmoidal dissepiments may also be present. Tabulae complete or incomplete, frequently with flat-topped domes. Increase usually lateral but may be axial.

TYPE SPECIES. *Diphyphyllum minus* F. A. Roemer (1855 : 29, pl. 6, figs. 12a-c). Frasnian, Ibergerkalk; Winterberg near Bad Grund, Harz, Germany.

DISTRIBUTION. Uppermost Givetian and Frasnian of Europe; ?upper Lower Devonian to Frasnian of Australia; ?Lower, Middle and Upper Devonian of North America.

DISCUSSION. In her original diagnosis, Soshkina (1939 : 23) included 'simple or composite, fasciculate and massive' corals and described the dissepimentarium as composed of 'one row of regularly spaced vesicles... sometimes flattened from above'. Soshkina (1954 : 32) later gave a slightly different diagnosis for the genus which Flügel (1956b : 355) mistranslated as excluding massive forms from *Peneckiella*. Schouppé (1958 : 191) pointed out Flügel's mistake but himself concluded that *Peneckiella* should be correctly defined (1958 : 192) as excluding massive forms. Both Flügel (1956b) and Schouppé (1958) gave extended discussions of this genus and concluded that it is characterised basically by a single, rarely double row of horseshoe dissepiments only in the dissepimentarium.

It is clear, however, from the holotype of *Peneckiella minor*, type species of *Peneckiella*, that it is peneckieloid (see Rózkowska 1960 : 32) and not true horseshoe dissepiments that are characteristic of the genus. No true horseshoe dissepiments can be positively identified in the holotype (Plate 17, figs. 4, 5), although they do occur in a subsidiary role in the dissepimentaria of some toptype specimens.

McLaren (1959 : 22) in the discussion of his new genus *Acinophyllum*, remarked that, from Frech's (1885 : 34, pl. 1, figs. 3, 3a, 3b) account of *Cyathophyllum minus* (F. A. Roemer), which was based on Roemer's specimen, 'it would appear likely that *Acinophyllum simcoense* is congeneric with *Diphyphyllum minus* and therefore with *Peneckiella*. But *D. minus* has been described several times since Frech and on no occasion has the description agreed closely with his.' In fact Frech's drawing (pl. 1, fig. 3a) more accurately portrayed the dissepimental structure of *D. minus* (except for the divergence of the septal trabeculae) than either Flügel's (1956b, text-fig. 1c) or Schouppé's (1958, text-figs. 13, 14) illustrations.

Dr. W. A. Oliver Jr. has kindly sent the writer two small fragments (BM(NH) R463661/-2) from a large colony of *Acinophyllum simcoense* from the Bois Blanc Formation (south quarry, Haldimand Quarries and Construction Ltd., north east of Hagersville, Ontario). Slides cut from this material show well developed peneckieloid dissepiments in longitudinal-section extremely similar to those of *P. minor*.

Where subsidiary dissepiments are developed, however, these are normal globose vesicles; no horseshoe dissepiments have been seen. The septal carination in cross-section is very variable and smooth septa do occur. Certainly the presence or absence of carinae cannot be considered to be of great significance here at the generic level. On all other characters, the specimen of *A. simcoense* can be placed with little doubt in *Peneckiella* and *Acinophyllum* is thus considered a junior synonym of that genus.

Rózkowska (1960 : 35) erected a new genus and species, *Sudetia lateseptata* which she considered (1960 : 50) to be a direct phylogenetic descendant of, and closely related to *Peneckiella*. The author is of the same opinion but believes that *Sudetia* does not warrant separate generic status.

Peneckiella, as suggested by Rózkowska (1960), apparently evolved from *Thamnophyllum*, chiefly by the fusion and modification of the horseshoe and flat dissepiments characteristic of the latter, leading to the diversification of dissepimental types found in *Peneckiella*. Besides the characteristic peneckielloid dissepiments, forms such as *P. minor kunthi* (Dames) (see Rózkowska 1960, text-fig. 27), *P. mesa* (Hill) (see Strusz 1965, text-fig. 156) and *P. salternensis* sp. nov. (see p. 274), include varying proportions of horseshoe, flat and sigmoidal dissepiments in their dissepimentaria. In fact, a morphological series can apparently be traced from a horseshoe and flat dissepimental pair, through sigmoidal to peneckielloid dissepiments. *P. minor sensu stricto*, with a fairly uniform peneckielloid dissepimentarium and only rare horseshoe dissepiments would appear to be an advanced form and *P. lateseptata*, as suggested by Rózkowska, a late stage form in this evolutionary trend.

***Peneckiella salternensis* sp. nov.**

Plate 18, figs. 1-4

1965 *Peneckiella* cf. *minor* (Roemer); Scrutton: 188, text-fig. 1.

DERIVATION OF NAME. After the type locality in Saltern Cove.

DIAGNOSIS. Phaceloid *Peneckiella*. Mean tabularium diameter 3.51 mm., mean corallite diameter 5.28 mm. with 17 to 21 major septa (topotype sample). Septa slightly and variably dilated; may be weakly carinate. Dissepimentarium dominated by peneckielloid dissepiments, but with horseshoe, flat and sigmoidal dissepiments also present. Tabulae regularly developed in form of wide, flat-topped domes. Increase lateral.

HOLOTYPE. OUM D548. Frasnian; thick bedded limestone immediately above igneous rock; southern end of Saltern Cove (SX 89505842), near Paignton, south Devon.

MATERIAL. Saltern Cove (main *Peneckiella* horizon); measured material: OUM D501, OUM D546-48, OUM D550-51, OUM D553; additional material: OUM D549, OUM D552. Saltern Cove (thin bedded limestones): OUM D554.

DISTRIBUTION. Frasnian; type horizon (main *Peneckiella* horizon) and from thin bedded limestones in the sequence immediately above, southern end of Saltern Cove, south Devon.

DESCRIPTION. Colonies are phaceloid with circular to sub-circular, close spaced corallites. External features are unknown as the specimens are preserved in a tough matrix. The epitheca is 0.1 mm. or slightly less in thickness.

The major and minor septa are variably dilated in the dissepimentarium, occasionally strongly spindle-shaped but showing all gradations to a virtually unthickened state. Their thickness ranges from about 0.3 mm. to 0.1 mm. or slightly less. The septa may be straight or zigzagged in this zone, and are sometimes variably carinate. Carinae are yardarm on straight septa and xyloid on zigzagged septa.

Minor septa end at the tabularium junction but the major septa, slightly attenuated, continue into the tabularium with a thickness of about 0.05 mm. or less. The major septa may be straight to slightly sinuous in the tabularium and normally extend about half way to the axis. Septal length is somewhat variable, however, and rarely they may more or less reach the axis or, conversely, only just penetrate into the tabularium. The axial ends of the major septa may rarely be slightly thickened.

The traces of one or two rows of dissepiments, uniserial between adjacent septa, may be seen in cross-section. The tabularium junction can be easily distinguished but it is not usually strongly defined.

In longitudinal-section, the dissepimentarium is composed of one or two series of highly variable dissepiments. The peneckielloid form dominates when the dissepimentarium is usually but not always uniserial. The occurrence of horseshoe dissepiments may be accompanied by peripheral flat dissepiments but normally the latter are very rare; horseshoes always occur in the inner row of biserial parts of the dissepimentarium. Sigmoidal dissepiments occur with about the same frequency as horseshoe dissepiments. The ratio of peneckielloid dissepiments to horseshoe dissepiments is highly variable from corallite to corallite, ranging between extremes of 2 : 1 and 10 : 1. The various dissepimental types are randomly distributed up the length of the corallites and the vertical spacing of the dissepiments may vary from 0.1 to 0.5 mm.

Tabularium structure is very constant, consisting of regularly and closely spaced, wide, flat-topped domes. Periaxial tabulae in the form of steeply dipping peripheral vesicles may sometimes occur. There are about 40 tabulae in 1 cm.

Increase is lateral corresponding closely to the 'thamnophylloid lateral' type described by Rózkowska (1960 : 31). The diameters of parent corallites displaying increase range from 5.3 to 5.6 mm.

A statistical analysis of the Saltern Cove material has been made but unfortunately individual colonies could not be distinguished. The statistics are listed in Table 15c and illustrated graphically in Text-fig. 21b.

DISCUSSION. *Peneckiella salternensis* can be distinguished from *P. lateseptata* (Rózkowska), *P. naliwkini* Soshkina and *P. achanaiensis* Soshkina on dissepimental character alone. The latter three are all characterized by almost exclusively uniserial dissepimentaria of uniformly developed peneckielloid dissepiments. *P. minor minor* (Roemer) apparently has a somewhat less regular dissepimentarium, with the presence of occasional horseshoes. The tabularium, however, although sometimes developing dome-shaped plates, shows tabulae irregularly developed and frequently depressed in the axial area. This is in strong contrast to the regularly

developed dome-shaped tabulae characteristic of *P. salternensis*. In addition, data given by Flügel (1956b : 359) for *P. minor minor* (Table 16) shows that subspecies to be smaller, with fewer septa than *P. salternensis*.

P. minor kunthi (Dames), *P. mesa* (Hill) and *P. boreensis* Strusz have dissepimentaria of similar complexity to *P. salternensis*. *P. minor kunthi*, however, has flat, or more commonly, incomplete, axially depressed tabulae and is smaller (Table 16) than *P. salternensis*. *P. mesa* and *P. boreensis* have flat-topped domes in their tabularia, but both Australian species have axial increase in contrast to the lateral increase in *P. salternensis*. In addition, *P. salternensis* is larger than *P. mesa* and *P. boreensis* (see Table 16) and the latter is further distinguished by excessive dilatation of the septa in the dissepimentarium.

TABLE 16.—Quantitative comparison of some species and subspecies of *Peneckiella*.

		d	dt	n
<i>P. salternensis</i>	O.R.	4.0-6.3	2.7-4.3	17-21
Paignton, S. Devon, England.	$\bar{x}$	5.28	3.51	19.91
<i>P. minor minor</i>	O.R.	3.5-4.9	2.9-3.9	15-18
Harz, Germany. 1	$\bar{x}$	3.9		
<i>P. minor minor</i>	O.R.	3.5-5.6	2.9-4.2	14-18
Antitaurus, Turkey. 1	$\bar{x}$	4.8		
<i>P. minor kunthi</i>	O.R.	2.5-4.8		12-18
Mokrzyszów, Poland. 2	$\bar{x}$			
<i>P. mesa</i>	O.R.	1.4-8.4	1.0-3.9	11-23
Wellington, N.S.W., Australia. 3	$\bar{x}$	3.6	2.12	17.00
<i>P. boreensis</i>	O.R.	0.9-10.1	0.7-6.5	3-28
Molong, N.S.W., Australia. 3	$\bar{x}$	4.5	2.8	16.00

Data from 1 Flügel, 1956b: 359.

2 RóŹkowska, 1960: 29.

3 Strusz, 1965: 557, 562.

Unfortunately data given for other species and subspecies of *Peneckiella* are not in a form allowing statistical comparison with the present material. Nevertheless they afford a valuable general indication of quantitative relationships and are therefore listed in Table 16.

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ADDENDUM

Whilst this paper was in press, J. E. Sorauf, (1967, *Paleont. Contr. Univ. Kans.*, **16** : 1-41) published a work describing phillipsastraeids from the Frasnian of Belgium. The opportunity is taken here to comment briefly on some of the more important points discussed by Sorauf which bear closely on the present paper.

Sorauf (pp. 5, 15) introduces the term "pseudocerioid", which he defines and uses in precisely the same way as in the present paper. It is gratifying to note that independent work by Sorauf and the writer on the same species (principally *Frechastrea goldfussi* and *F. pentagona*) has led to the same interpretation of the corallite wall structure. Sorauf (p. 5), however, infers that species of *Phillipsastrea* and the Phillipsastraeidae are never cerioid whereas the genus and family as defined here do include massive forms with an epitheca between at least some of the corallites (this paper, p. 210).

Sorauf (p. 13) separates *Phillipsastrea* and *Pachyphyllum* by restricting the latter genus to species with a perfect single series of horseshoe dissepiments. In *Phillipsastrea* he includes a complete range of dissepimental form, from specimens lacking any sign of horseshoe dissepiments to those in which an almost complete series is present. In fact this whole range is represented in Sorauf's concept of a single species of *Phillipsastrea*, *P. hennahi* (fig. 5, 1c and 2).

Apart from the difference in the degree of development of the horseshoe dissepiments, species of *Phillipsastrea* and *Pachyphyllum* show no significant divergence in their basic morphology to warrant generic separation. Moreover, when the development of horseshoe dissepiments is closely examined even this criterion is, in the writer's opinion, impossible to maintain (compare the longitudinal-section of a topotype of *Pachyphyllum bouchardi* (Semenoff-Tian-Chansky 1961, pl. 9, fig. 2) with a section attributed by Sorauf (fig. 5, 2) to *Phillipsastrea hennahi*).

The writer is also unable to agree with Sorauf's (p. 26) interpretation of *Phillipsastrea hennahi*. None of the illustrations (figs. 5, 1a-c; 8, 1a-d: figs. 5, 1d-e; 5, 2 are longitudinal-sections only) is considered consubspecific with *Phillipsastrea hennahi hennahi* herein, whilst two specimens (figs. 5, 2; 8, 1a-b) are possibly consubspecific with *P. hennahi ussheri* subsp. nov. The significance of this should not be overlooked. *P. hennahi hennahi* appears to be characteristic of the middle and upper Givetian of England (this paper, p. 216), not of the Frasnian as stated by Sorauf (pp. 23, 27). On the other hand, the subspecies *P. hennahi ussheri* is found in the English Lower Frasnian.

The same English Lower Frasnian limestones yield *Frechastraea pentagona pentagona* and *F. pentagona minima*. Both subspecies were considered, the latter by inference, to be upper Frasnian index forms by Sorauf (pp. 31, 33).